The Surge Flies (Diptera: Canacidae: Zaleinae) of Australasia and Notes on Tethinid-Canacid Morphology and Relationships

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ABSTRACT. The morphology, relationships, and classification of the Tethinidae and Canacidae are considered, with special reference to the Zaleinae. Homologies of bristles near the vertex of the head are critically appraised, and the origin of the sclerite known as the prelabrum or anteclypeus is considered. The family Canacidae Jones, 1906 is classified into the following six subfamilies: Apetaeninae Mathis & Munari, 1996; Canacinae s.str.; Horaismopterinae Sabrosky, 1978; Pelomyiinae Foster, 1976; Tethininae Hendel, 1916; Zaleinae D. McAlpine, 1985. The family name Tethinidae thus becomes a new subjective synonym of Canacidae. The subfamily Nocticanacinae Mathis, 1982 becomes a tribe Nocticanacini n.stat. of Canacinae. *Tethinosoma* Malloch is transferred from the Tethininae to the Horaismopterinae. A key to subfamilies of Canacidae *s.l.* is given. A revised characterization of Zaleinae is given and its two genera and c. 16 species are keyed. Revised characterizations of *Suffomyia* Freidberg and *Zalea* D. McAlpine are given. The following new species are described: *Suffomyia sabroskyi* (Caroline Islands); *Suffomyia ismayi* (New Guinea); *Zalea earlyi, Zalea johnsi, Zalea lithax, Zalea mathisi, Zalea ohauorae, Zalea uda, Zalea wisei* (New Zealand); *Zalea clava* (Western Australia); *Zalea dayi* (New South Wales). Two doubtful species represented by inadequate material are assigned provisional numbers. Adults of these maritime flies were found on shoreline rocks or on stranded "seaweed". Parasitism of four *Zalea* spp. by laboulbenialean fungi is recorded. Collection techniques for zaleines are mentioned.

As explained below, the family concepts Canacidae and Tethinidae are here combined as a single family, the former (as Canacenae Jones, 1906) having nomenclatural priority over the latter (first given as Tethinidae Hendel, 1916). See Sabrosky (1999) for details. The family name Tethinidae is therefore no longer used except in reference to older usage. To avoid confusion, I here refer to the new expanded concept of Canacidae as "Canacidae *s.l.*", and to the narrower traditional concept of Canacidae, excluding the "tethinid" taxa and the Zaleinae (i.e. the Canacinae plus the Nocticanacinae sensubus Mathis, 1992), as the subfamily Canacinae *s.l.* The subfamilies of "Tethinidae" used by Mathis & Munari (1996), viz. Apetaeninae, Horais-mopterinae, Pelomyiinae, Tethininae, and Zaleinae, are retained as a further five subfamilies of Canacidae *s.l.*

This paper records an increase in the number of known species of Zaleinae from four to about 17, though two of these remain unnamed because of inadequate material. New Zealand has a remarkably high representation with about 10 species seen so far, though the collections are meagre. Numerous species have probably been overlooked here and elsewhere in the Pacific because of their small size and specialized habitat. It is hoped that a New Zealand resident will undertake a major study of zaleines using ample material. Even in Australia there are still no species recorded for Queensland and South Australia, though they are very probably present.

Zaleine flies should be sought on intertidal rock-outcropping in the splash zone. We use a strong sweep net with nylon-voile bag and protective calico skirt. This is swept particularly in or over wet rock crevices or likely surfaces. The flies are extracted with an aspirator while wearing a low-power binocular magnifier. They may be collected directly into 80% ethanol. However, experience shows that dry specimens are more suitable for permanent record. These specimens are collected into dry glass containers, and, immediately after killing (e.g., with chloroform vapour or by freezing), the abdomens of both sexes must be fully extended with fine forceps to enable taxonomic study. Hazards of collecting in this habitat are the same as for rock-fishermen.

Terminology and abbreviations

In descriptions I generally follow a traditional terminology with minimal use of terms implying doubtful, unproved, or, for present purposes, irrelevant homologies. Details are given by D. McAlpine (1973), and for the male postabdomen by D. McAlpine (1985b). Most terms are also explained by Harrison (1959), Crosskey (1973), and Colless & D. McAlpine (1991). Paired structures are described in the singular, except where the context makes this inappropriate. The antenna is treated as a six-segmented appendage, and the segments (including those of the arista) are numbered consecutively from the base. Cell-4 index is defined as the ratio of the length of the antepenultimate section of vein 4 to the full length of the discal cell along vein 4. Other terms are explained below.

The Canacinae *s.l.* have been called "beach flies" in some modern literature, in contrast to the "shore flies" (Ephydridae), with which these were usually conflated in older literature. The tethinids have also been called "beach flies" (e.g., by Munari, 2000), so that the term has application to the more inclusive concept of Canacidae *s.l.*, although some species do not inhabit beaches. I believe that such vernacular group names, if consistently applied, can be useful in communicating with non-specialists and non-entomologists, especially those concerned with research funding and conservation ecology. I introduce the term "surge flies" (German Brandungsfliegen) for the Zaleinae, in reference both to their habits and to the derivation of the scientific name (Greek *zale* = the surge of the sea).

Institutions housing specimens are abbreviated as follows:

AM	Australian Museum, Sydney
AMNZ	Auckland War Memorial Museum, Auckland
ANIC	Australian National Insect Collection, CSIRO, Canberra
BM	The Natural History Museum, London
BPB	B.P. Bishop Museum, Honolulu
CMC	Canterbury Museum, Christchurch
CNC	Canadian National Collection, Agriculture Canada, Ottawa
MCV	Museo Civico di Storia Naturale, Venice
NAT	Natal Museum, Pietermaritzburg
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland
TAU	Department of Zoology, Tel Aviv University, Tel Aviv
TDA	Department of Primary Industries, New Town, Tasmania
USNM	National Museum of Natural History, Washington, D.C.
ZMC	Zoological Museum, Copenhagen

Morphological study for this paper has been performed using a stereo light microscope (SLM), compound light microscope (CLM), and scanning electron microscope (SEM).

The following collectors' names are abbreviated to the initials: D.J. Bickel, B.J. Day, J.W. Early, D.S. Horning, J.W. Ismay, D. Mathis, W.N. Mathis, D.K. McAlpine, R. Meier, C.W. Sabrosky, K.A. Wise.

Notes on biology and ecology

The Zaleinae, like most other canacid flies, are restricted to the sea shore. I have been involved in the collection of seven species of *Zalea*, and these were on shoreline rocks, never on beaches or nearby vegetation. I previously gave habitat notes for adult *Zalea*, based mainly on observations of *Z. minor* (D. McAlpine, 1982). These are confirmed by my subsequent observations on this and other species, except that a general association of *Z. minor* or other *Zalea* spp. with calcareous worm tubes is not confirmed. On one occasion *Z. major* was found to be particularly numerous on intertidal rocks encrusted with barnacles and splashed by the incoming tide at "The Ruins", Booti Booti National Park. Numbers of *Z. clava* were swept from the roof of a tunnel-like overhanging rock, continuously wet from heavy wave action, at the foot of cliffs near Cable Beach, S of Albany. They were associated in this habitat with the coelopids *Chaetocoelopa sydneyensis* (Schiner) and *Lopa convexa* D. McAlpine. The rocks from which *Zalea* spp. have been obtained were almost always wet from wave action or occasionally from rain. Numbers of *Z. minor* were once found at Kurnell, near Sydney, under a rock overhang above high tide level, during high tide when the intertidal rock platform was submerged. These habitat preferences would ensure that the flies are not subjected to even moderately high temperatures or low humidity. They also indicate that the flies are uninjured by heavy splash from waves.

Habitat data from *Suffomyia* spp. indicate less strict association with rock surfaces than for *Zalea*. Freidberg (1995) states for *S. scutellaris*: "All the specimens were swept at sandy or rocky beaches, usually covered in part with algal mats or other organic debris. They were confined to the immediate vicinity of the water (within half a meter) at the 'intertidal zone'". Label data for *S. ismayi* say: "swept decaying seaweed". All specimens of *S. sabroskyi* were collected "at light", so the natural habitat is not recorded.

Ectoparasitic fungi of the order Laboulbeniales are frequent on *Zalea minor*, *Z. major*, and *Z. dayi* at some localities in New South Wales, and also occur on *Z. clava* in Western Australia (see Figs 46, 47). The fungal ascomata are most frequently attached to the ventral surface of the basal third of the wing, also commonly to the legs, and one specimen of *Z. minor* has a cluster of ascomata on one halter. Heavy infestations must hamper some of the flies' movements, but, as the fungus does not attack internal organs, it is not normally fatal.

Attempts to obtain larvae of zaleines have so far been unsuccessful. It is probable that they live in a sheltered microhabitat in the intertidal zone.

Morphology

I treat here the comparative morphology of certain structures, particularly those which have value in the classification of the Canacidae *s.l.* or of the Chloropoidea, sensu Colless & D. McAlpine (1991).

The prelabrum or anteclypeus. I here maintain the term prelabrum for the transverse (on each side posterolaterally extended) sclerite between the face and the labrum, in most cyclorrhaphans. This is because I cannot decide from the evidence immediately available whether it is a part of the clypeus or a sclerite of separate origin. The sclerite was termed anteclypeus by Crampton (1942), although, according to his hypothesis, it should be a posterior element of the clypeus, being farther from the antennae (which represent the primitive segment 1 of the insect head). It was unfortunately termed simply clypeus by J. McAlpine (1981), following several precedents.

The study of the facial region of the Brachycera has been inadequately considered in major works on morphology and phylogenetic classification. My own brief comparative study leaves little room for doubt that the clypeus, either wholly or in substantial part, is incorporated into the area of the cyclorrhaphous head capsule called the face by modern dipterists. If the cyclorrhaphous prelabrum is of clypeal origin, then it represents a small ventral section of the original clypeus which has become more are less detached from or hinged with the rest of the clypeus in the formation of the flexible proboscis. This appears to be the view of Crampton (1942), but no substantial evidence has been offered for preferring this interpretation over that of independent sclerotization.

In orthorrhaphous brachycerans, possession of a sclerite resembling the prelabrum is of restricted occurrence, and such sclerite is possibly absent in the groundplan of the Brachycera. Such groundplan condition probably resembled that of the rhagionid genus *Atherimorpha* White (Fig. 1). An obvious sclerite resembling the prelabrum is visible in most taxa of Stratiomyidae which I have examined, including the rather plesiomorphic chiromyzines (see Crampton, 1942: fig. 1L, ac). A sclerite resembling this to a variable extent is present in some taxa of Bombyliidae. It may be considered that these are isolated occurrences in taxa phylogenetically remote from the Cyclorrhapha, so that any similarity to the latter is likely to be convergent. The nearest outgroups to Stratiomyidae, according to recent sources (e.g., Sinclair, 1992) are the Pantophthalmidae and particularly the Xylomyidae. In my limited material of these two families, I can detect no distinct prelabrum.

Among the Empidiformae (formerly Empidoidea), the prelabrum is absent in many taxa. In *Syneches* spp. (Hybotidae) there is an apparent prelabrum, which forms a flat sclerite on the subcranial membrane and is anteriorly joined to the lower margin of the face. Krystoph (1961: fig. 1) figured such a sclerite for *Empis* sp. (Empididae), which he identified as the clypeus. More prominent structures sometimes resembling a prelabrum in certain empidiforms are apparently the true labrum (Krystoph, 1961).

The primitive cyclorrhaphan *Ironomyia nigromaculata* White (Ironomyiidae, Fig. 2) probably shows the face and prelabrum in a condition close to that of the groundplan of the Cyclorrhapha, or the prelabrum in a condition transitional between such groundplan and that of the higher
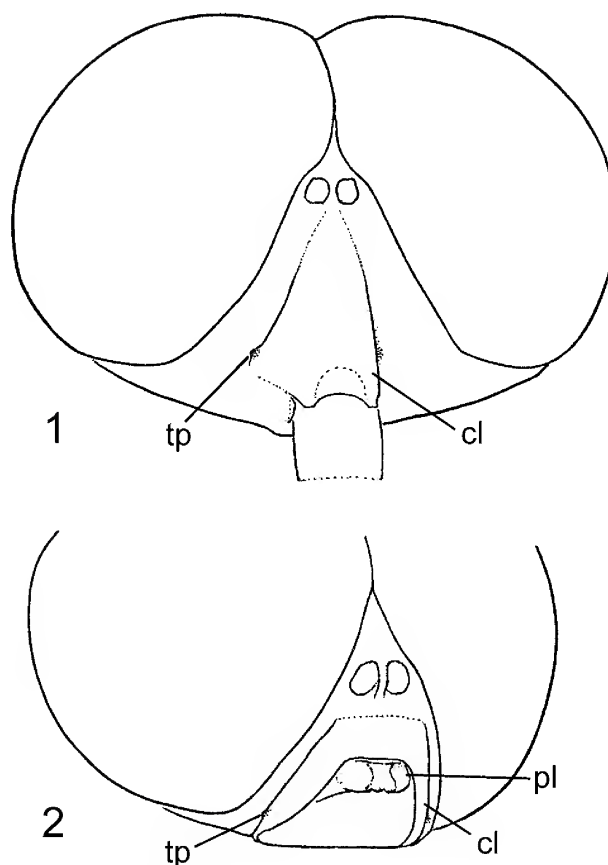

Figs 1–2. (*1*) *Atherimorpha* sp., outline of head of male. (*2*) *Ironomyia nigromaculata* White, outline of lower part of head of male. *cl*, clypeus; *pl*, prelabrum; *tp*, tentorial pit.

cyclorrhaphans (including Syrphidae and Schizophora). Most other taxa of the grade Aschiza have undergone partial desclerotization, suture reduction, or other modifications. *Ironomyia* retains the primitive clypeal sutures with a little modification in position, in addition to having a distinct prelabrum, but the latter is very weakly sclerotized medially. I therefore regard it as a significant indicator of at least some homologies between schizophoran and lower brachyceran structures as indicated in Fig. 2. J. McAlpine (1981: 19) stated: "Peterson (1916) wrongfully interpreted the reduced clypeus [i.e. the prelabrum] in the Muscomorpha [i.e. Cyclorrhapha] as tormae." Perhaps the bipartite nature of the prelabrum of such primitive cyclorrhaphans as *Ironomyia, Melanderomyia* Kessel, and *Sciadocera* White provides evidence of its origin from a pair of sclerites such as the tormae.

There is a tendency in the Cyclorrhapha for the tentorial pit, located on the lateral arm of the fronto-clypeal suture, to move on to the ventral surface of the head capsule, carrying with it a ventral extension of the suture. The part that I have designated the hypofacial in *Zalea* (D. McAlpine, 1982: fig. 3) and many other schizophoran taxa is perhaps a lateroventral extension of the clypeus.

Facial structure. The structure of the face in the canacid-tethinid taxa can be classified in three main categories.

Type 1. In the Apetaeninae, Zaleinae, and most genera of Tethininae (e.g., *Pseudorhicnoessa*, Fig. 3) the face is generally rather weakly sclerotized, almost vertical, not
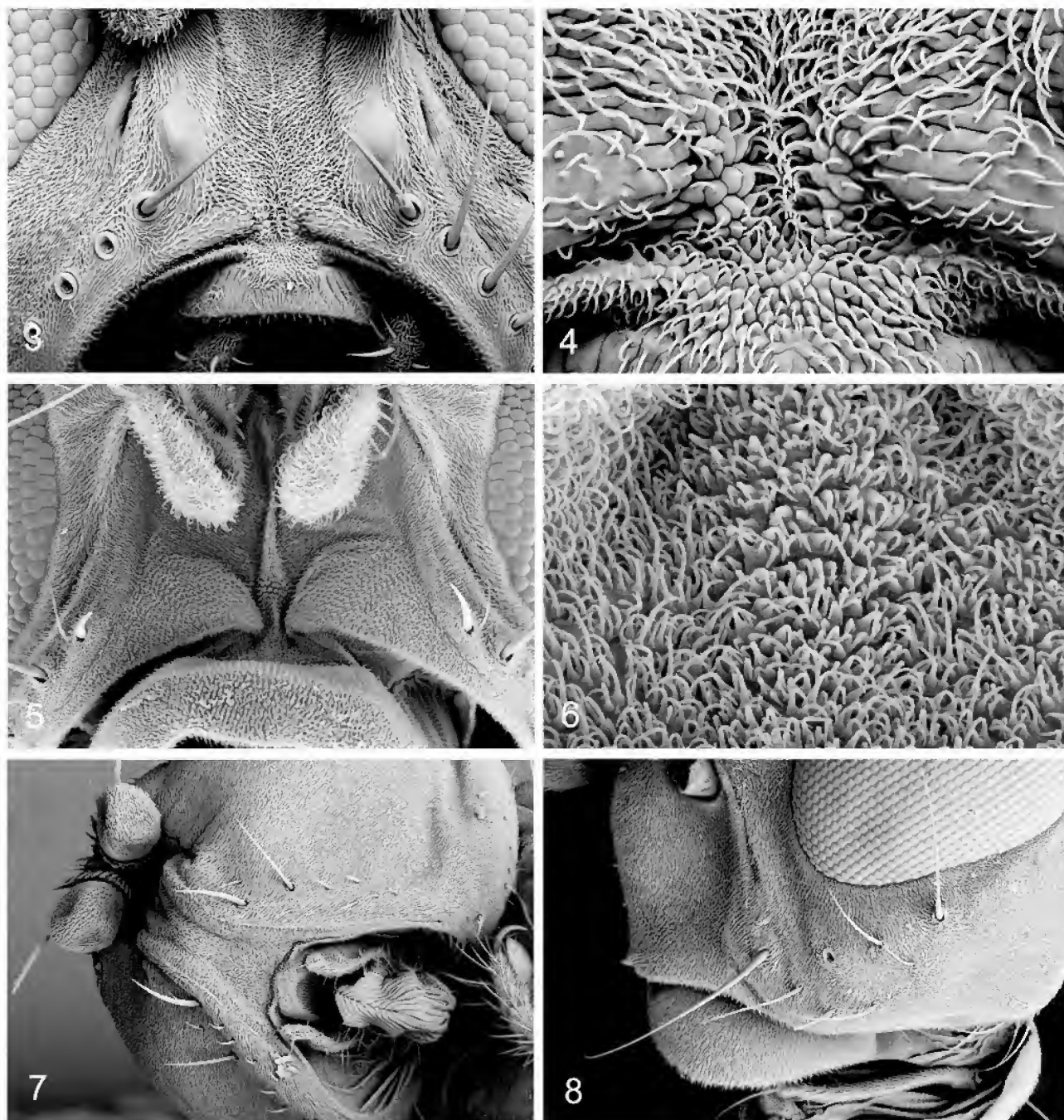
Figs 3–8. (*3*) *Pseudorhicnoessa* sp., face and adjacent parts. (*4*) the same, detail of lower margin of face, showing bulbulate cuticle. (*5*) *Apetaenus (Macrocanace) australis* (Hutton), face and adjacent parts. (*6*) the same details of lower margin of face. (*7*) *Tethinosoma fulvifrons* (Hutton), head, ventral-oblique view. (*8*) *Canace salonitana* Strobl, cheek, face, and adjacent parts, lateral view.

noticeably convex, and terminates ventrally at the junction of the anterior and ventral surfaces of the head capsule. Its surface thus has no more or less ventrally facing component, and the prelabrum (always close to its defined lower or epistomal margin) is not displaced posteriorly. Also the face is narrowly desclerotized on the median ventral part, so that the visible lower margin in interrupted medially to a variable extent (see Hennig, 1971: fig. 73, and my Figs 4–6).

Type 2. In the Pelomyiinae and Horaismopterinae (e.g., *Tethinosoma*, Fig. 7) the face is uniformly rather weakly sclerotized (or in *Horaismoptera* quite strongly so), with its lower margin entirely defined and displaced on to ventral surface of head, so that the prelabrum is also posteriorly displaced. The face may be relatively narrow (*Pelomyia, Tethinosoma*) or extremely narrow (*Pelomyiella*). The face of *Neopelomyia* seems atypical of the Pelomyiinae, but without more material I cannot interpret all the details.

Type 3. In the Canacinae *s.l.* (Fig. 8) the face is uniformly strongly sclerotized and convex in horizontal section, so that in profile its median line forms part of the outline of the head. The sharply defined lower margin does not recede on to the ventral surface of the head, so that the prelabrum is situated well forward as in type 1.

In the genus *Tethina s.l.* (including *Rhicnoessa*) there is much variation in facial structure in the limited available material. In *T. carioca* Prado & Taveres, the face is more
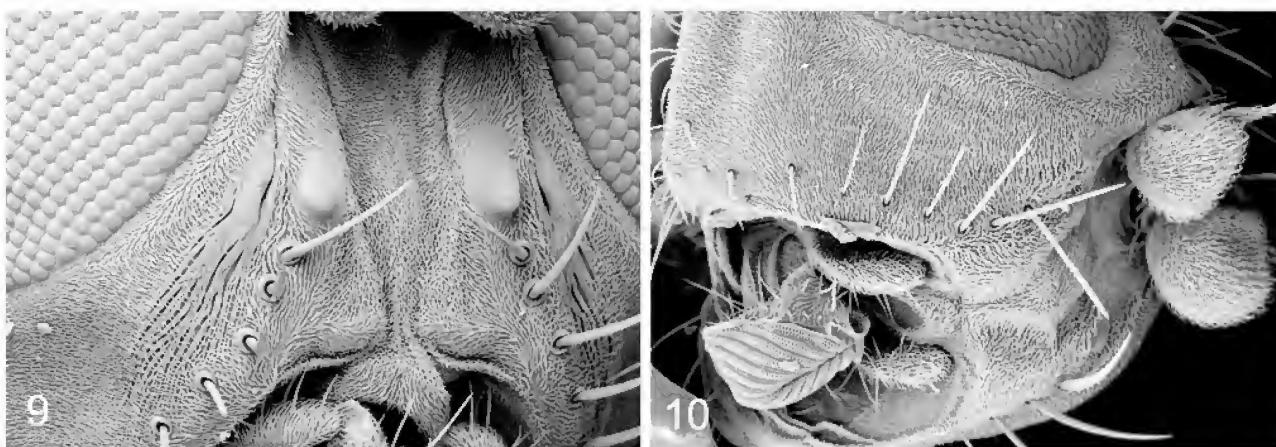
Figs 9, 10. (*9*) *Tethina nigriseta* Malloch, face and adjacent parts. (*10*) *Tethina pallidiseta* Malloch, cheek region and adjacent parts.

uniformly sclerotized than in *Pseudorhicnoessa* spp., its surface largely approximating to a vertical plane, with a slight median carina from a little above centre to near lower margin, which becomes broader and more tumid below and is defined by a shallow groove on each side. Only a very narrow ventral marginal zone is reflexed so as to face ventrally, and the prelabrum is not markedly displaced posteriorly. In *T. horripilans* (Melander) the facial structure is similar to the above, but the paired grooves are broader and apparently desclerotized, delimiting a convex, subtriangular median sclerite immediately above lower margin, which is narrowly prolonged above. The above description is based on a female specimen in which the median sclerite is particularly well defined and pigmented. In a male of *T. horripilans* the median sclerite is smaller and less defined, but there remains the sharp distinction between the sclerotized lateral facial plates and the desclerotized paramedian zones. In *Tethina pallidiseta* Malloch, from examination of numerous well sclerotized specimens in which no part of the face has collapsed in drying, (SLM and SEM) there is not only departure from structural type 1 but also from that of most available *Tethina* spp. (see Fig. 10). Instead of having almost the whole depth of the face almost vertical, it has a substantial ventral area of the face receding on to the ventral surface, or at least the anteroventral surface of the head. Thus, the distinctly visible ventral margin of the face and the prelabrum are located well back on the ventral surface of the head. The c. vertical anterior surface of the face is very similar to that of *T. carioca* described above, with low, ventrally widened median carina flanked by a pair of grooves, and with largely nearly uniform weak sclerotization; but in *T. carioca* this vertical surface forms almost the whole surface of the face. In *T. nigriseta* Malloch (Fig. 9) the facial structure is, to some extent intermediate between that of *T. carioca* and *T. pallidiseta*. The lower part of the face recedes only slightly, so that posterior displacement of the prelabrum is correspondingly slight. The median carina is relatively weakly developed. The unifying feature through all available *Tethina* spp. is the presence of the median carina, not seen in other genera of Tethininae.

Determination of phylogenetic polarity in facial characters is difficult in the canacid-tethinid complex because the probable outgroups, Chloropidae (e.g., Fig. 11) and Milichiidae, are themselves variable. However, with reference to what are likely to be cladistically stepped outgroups, and with elimination of those with probably autapomorphic facial conditions, a groundplan condition for both Chloropoidea and Canacidae *s.l.* (assuming monophyly for both categories) is likely to include the following features: face almost uniformly moderately sclerotized, not markedly convex or protuberant, in profile nearly vertical or, perhaps, slightly concave, not receding below, with well defined ventral margin, which is quite narrowly separated from prelabrum.

On this basis, none of the above three types of facial structure is entirely plesiomorphic. Type 1 is apomorphic in the ventromedian desclerotized zone and associated discontinuity of the ventral margin. Type 2 is apomorphic in the markedly receding lower part of the facial surface, and associated posterior displacement of the lower margin. Type 3 is apomorphic in being strongly convex in horizontal section. Thus facial structure supports to some extent the subfamily classification here followed.

The cuticle of the sclerotized lower lateral areas of the face in *Pseudorhicnoessa*, etc. is microtrichose and partly crazed (cf. that of the diopsid *Centrioncus* Speiser, see D. McAlpine, 1997), but, on the median emargination of the face and the area immediately below, the sclerotization is broken into many separate bulblet-like structures each bearing one microtrichium (Fig. 4). This relatively flexible type of cuticle I term bulbulate, from botanical Latin *bulbulus*, a small bulb or bulblet, as occurs in the axils of some plants. Such bulbulate cuticle occurs on much of the face in *Apotropina* sp. (Chloropidae, Siphonellopsinae, Fig. 11) and, in a slightly modified form, in *Cadrema* sp. (Chloropidae, Oscinellinae).

On the assumption that the bulbulate cuticle is homologous in both Tethininae and Chloropidae, its presence in the groundplan of the Chloropoidea is inferred. Unfortunately face microstructure, has not been investigated in most other schizophoran families.

In *Tethina* and several other genera of Tethininae there is a shining tubercle on the facial ridge (sensu Crosskey, 1973) just above the vibrissa. In *Horaismoptera* there is no such separate tubercle, but the vibrissal socket is located on a shining convexity. Shining, glabrous prominences or ridges on the facial or cheek region occur in numerous fly taxa, notably in *Apotropina* Hendel (Chloropidae), *Coelopella* Malloch, *Dasycoelopa* Malloch, *Malacomyia* Westwood, *Rhis* D. McAlpine (Coelopidae), *Hecamede* Curtis
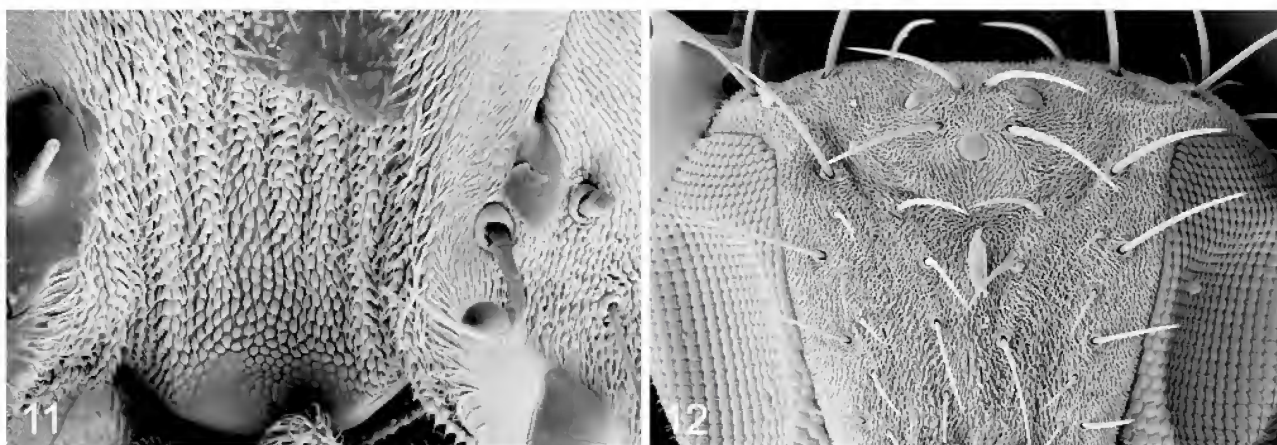
Figs 11, 12. (*11*) *Apotropina* "sp. M" (in AM), detail of lower part of face. (*12*) *Tethina pallidiseta* Malloch, postfrons. Postvertical bristle indicated.

(Ephydridae), *Helcomyza* Curtis, *Maorimyia* Tonnoir & Malloch (Helcomyzidae), *Heterocheila* Rondani (Heterocheilidae). These genera all live in sandy habitats, though perhaps this does not apply to all species of *Apotropina*.

I have found adults of *Apotropina exquisita* (Malloch) and *A. ornatipennis* (Malloch) on loose sand of coastal dunes. Some other species of the genus are associated with burrowing Hymenoptera (Ferrar, 1988), where they probably also face risk of burial. Perhaps these shining prominences are used by flies in pushing their way through sand, as occasional accidental burial must occur in these habitats. Adults of *Rhis whitleyi* D. McAlpine burrow in sand below stranded kelp, when disturbed (author's observations).

Bristles on the upper back of the head. Hendel (1916) made a useful comparative study of what he called the *Postvertikalborsten* in acalyptrate Diptera, and indicated their importance in family classification, though the English term "post-vertical" was used for the same bristle pair as early as 1884 by Osten-Sacken. General usage of the term postvertical bristle continued until Steyskal (1976) proposed to substitute the term postocellar bristle, on grounds that are no more than a personal preference. Unfortunately Steyskal's substitution was adopted in the influential Manual of Nearctic Diptera (see J. McAlpine, 1981), contrary to most usage over the previous 90 years. I propose to continue usage of postvertical bristle for these bristles among such families as Drosophilidae, Heleomyzidae, Lauxaniidae, Piophilidae, and Sciomyzidae, where their homology is not in dispute.

There is currently a problem with the identification of the postvertical bristle (syn. postocellar sensu Steyskal) in the tethinid-canacid complex.

For *Tethina cinerea* (Loew), Hendel (1928: fig. 179) labelled the pseudopostocellar bristles (of later authors) as postocellars (poc), and he labelled the convergent bristle pair (here interpreted as postverticals) as inner occipitals (occi), without recognizing any postvertical bristles. For numerous other families, including Carnidae and Milichiidae, he labelled the one pair of bristles directly behind the ocelli as postverticals (pvt). In the absence of any discussion of these points in Hendel's work, it seems that his reticence in applying the term postvertical to any bristle of the head of *Tethina* may have been due to indecision as to which bristle pair is homologous with the postverticals of other families. Probably the only recognized tethinids to which Hendel had

access in 1928 were relatively few species of Tethininae and Pelomyiinae.

Vockeroth (1987) stated for the Tethinidae: "postocellar bristles absent; inner occipital bristles moderately strong to minute, slightly to strongly convergent." Wirth (1987) stated for the Canacidae: "postocellar bristles absent, but often replaced by pseudopostocellar bristles, i.e. specialized ocellar setulae." Munari (1999, following J. McAlpine, 1989) stated for the Tethinidae: "paraverticals (pavt = poc or pvt of some authors) very weakly developed to relatively strong, usually widely separated and convergent (divergent only in Zaleinae) simulating true postocellars [sic] setae;" ... "ocellar setae ... sometimes combined with a posterior pair of additional, widely divergent hairs (pseudopostocellars setae, sensu J. McAlpine, 1989)." Hendel's and Vockeroth's "inner occipital bristles" and Munari's "paraverticals" are the same concept. Steyskal (1976) introduced the term paravertical bristle for a bristle placed laterad of the postocellar (postvertical) and mesad of the inner vertical, occurring in certain calyptrate and pseudopomyzid flies.

I have examined all major groups of the tethinid-canacid complex to test the viewpoint that postvertical bristles are uniformly absent and generally replaced by paravertical bristles in these taxa. The taxa of this complex have at most one pair of bristles in this region (i.e. excluding the pseudopostocellars), which are convergent except in some (not all) Zaleinae, and which range from far apart (in *Horaismoptera* and *Pseudorhicnoessa*) to quite close together (in *Tethinosoma*), through a range of intermediate positions in *Tethina* (Fig. 12), *Dasyrhicnoessa, Pelomyia, Macrocanace*, and *Zalea* (Fig. 13). There is much evidence of variation in position of insertion of the bristle, but none of separate origin of such a bristle in different taxa. It is therefore logical to treat these as the same homologous bristle pair through all these taxa. But I can find no shred of evidence for regarding them as non-homologous with bristles identified as postverticals (or postocellars) in such outgroups as Chloropidae, Coelopidae, and Lauxaniidae. Paravertical bristles sensu Steyskal possibly occur in no family closer than the Pseudopomyzidae and certain Heleomyzidae (e.g., *Borboroides* Malloch) and Sphaeroceridae, where they may have arisen independently and occur beside typical postverticals. I therefore dismiss as a fallacy, based in inadequate comparative study, the claim that paravertical bristles are present in the tethinid alliance, and I revert to the
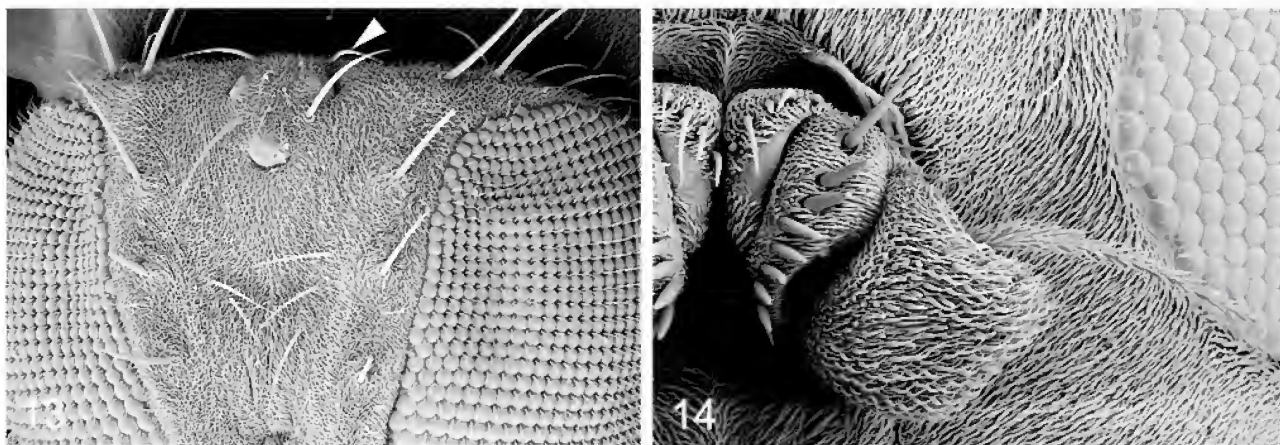
Figs 13, 14. (*13*) *Zalea dayi* n.sp., postfrons. Postvertical bristle indicated. (*14*) *Tethinosoma fulvifrons*, antenna.

formerly used term postvertical. Postvertical bristles, in this sense, are absent in the Canacinae *s.l.* and in some species or specimens of Apetaeninae.

I know of no better term than pseudopostocellar bristles, as used by Wirth (l.c.), for the pair of closely placed, divergent bristles in front of the postverticals, which are evidently derived from setulae of the ocellar region. These are distinct in many taxa of Canacinae (*s.l.*) and Tethininae, in the latter group in addition to convergent postverticals (see Fig. 12).

Previously (D. McAlpine, 1982), I described the postvertical bristles of *Zalea* as "widely spaced, proclinate, divergent or subparallel", and compared them with the divergent "postvertical" bristles of the Canacidae s.str. Freidberg (1995) described *Suffomyia scutellaris* Freidberg as having "pseudopostocellar setae", but "postocellar, paravertical and inner occipital setae lacking", again homologizing this bristle pair through Zaleinae and Canacinae, though using a different term. I am now satisfied that both our interpretations are incorrect. The pseudopostocellars when present in Canacinae *s.l.* are closely approximated, and often tend to be only slightly differentiated from the relatively numerous and irregular ocellar setulae, often not transversely aligned, and sometimes duplicated. What I regard as postvertical bristles in the Zaleinae are at least as far apart as the posterior ocelli, well removed from the small ocellar setulae, and generally quite regularly placed. But for the fact that they are commonly divergent, they are similar to the postvertical bristles of the Pelomyiinae. I therefore identify these bristles of Zaleinae as true postverticals, in contrast to the pseudopostocellar bristles of Canacinae *s.l.*

Zalea horningi and some closely related species differ from other zaleines in that the postvertical bristles are convergent. This is the normal condition in other subfamilies of Canacidae *s.l.* and of the outgroups Milichiidae and Chloropidae, and is the probable groundplan condition for the Canacidae *s.l.* But if *Z. johnsi* is closely related to the *Z. horningi* alliance, it appears that the non-convergent condition is a groundplan autapomorphy for Zaleinae and that the state in *Z. horningi* is a reversal, on the evidence of three stepped outgroups, viz. *Zalea johnsi*, other species groups of *Zalea*, the genus *Suffomyia*.

The antenna. In *Horaismoptera* and *Tethinosoma* antennal segment 2 (the pedicel) is remarkably short and robust, with

a series of short, stout spines or spinescent setulae on the distal margin of the inner surface (Fig. 14). The antennae are directed outwards from their bases, and thus diverge more markedly than in such possibly related genera as *Pelomyia*, so that the group of spines or stout setulae is prominently exposed. In the specimen of *Tethinosoma fulvifrons* examined with SEM, the apices of these bristles appear to be abraded. Here we have a similar condition to that of the platystomatid *Rhytidortalis averni* D. McAlpine and related species (D. McAlpine, 2000), where, in the female only, there is a well-developed comb on antennal segment 2, of which the spinescent bristles can show similar apical abrasion. The equal development of the antennal modification in both sexes of *Tethinosoma* perhaps makes its primary use here in intraspecific agonistic behaviour improbable. It is reminiscent of the rastellum on the chelicera of certain spiders, which is generally considered to be a digging organ. The term rastellum, as used in Arachnology, may therefore be applied to this rake-like group of spines in *Tethinosoma* and *Rhytidortalis* spp. As both *Tethinosoma* and the relevant *Rhytidortalis* spp., probably also *Horaismoptera* spp., are restricted to sandy coastal habitats, the antennal rastellum in these may have the common function of digging through or extrication from loose sand, as surmised above for certain facial modifications. Perhaps the particular development of the rastellum in the female only of *Rhytidortalis* spp. is due to more frequent or intimate contact with sand during oviposition, as the larvae are strongly suspected of being associated with roots of dune plants.

The prosternum. The prosternum in the Schizophora is commonly represented by two sclerites—the small anterior presternum and the larger posterior basisternum (Speight, 1969: fig. 12). The basisternum is often simply called "prosternum" in the literature, because it is often more readily viewed in dried material without decapitation (Figs 15–22).

The presternum in what is probably the primitive condition for the Chloropoidea (sensu Colless & D. McAlpine, 1991) is a small rounded sclerite close to or connected to the middle of the anterior margin of the basisternum (Figs 17, 18). Such a presternum occurs in *Tethina pallidiseta* Malloch, *Tethinosoma fulvifrons* (Hutton), and various other taxa of Canacidae *s.l.* In the subfamily Canacinae the presternum is often vestigial. In the Zaleinae the presternum is variable, but is always well developed. In
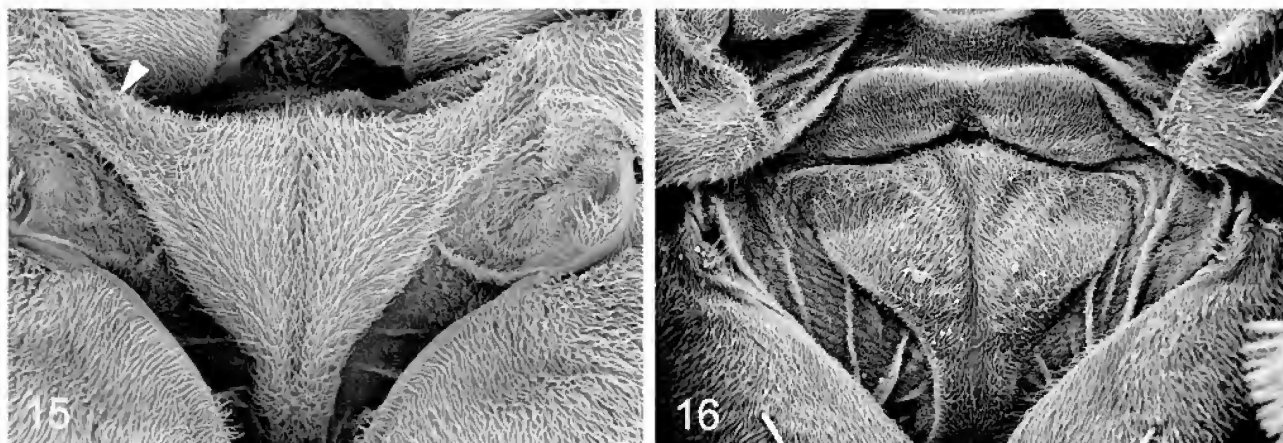
Figs 15–16. (*15*) *Zalea johnsi*, prosternum showing precoxal bridges, presternum concealed. (*16*) *Z. minor*, prosternum (unbridged) and adjacent parts.

Zalea horningi (Fig. 20), *Z. johnsi* (Fig. 15), and *Z. lithax* the presternum is small, though notably broader than in *Tethina*. In *Z. wisei* and *Z.* sp. 1 (Fig. 21) it is broader. In the four Australian *Zalea* spp. (e.g., *Z. major*, Fig. 22; *Z. minor*, Fig. 16) the presternum is very broad, with a median groove, and there is a narrow transverse membranous zone separating it from the basisternum. I studied the prosternal region in *Z. major* and *Z. minor* in freshly killed specimens in which the membranous cuticle was still fully flexible and the degree of separation of sclerites could be satisfactorily demonstrated. The above description is therefore more accurate than my previous statement, based on dried specimens, that the prosternum of *Zalea* has "median and transverse sutures forming a cruciate complex" (D. McAlpine, 1982). Although

the prosternum of *Suffomyia sabroskyi* is in general narrowed, the presternum is not particularly so, being about as broad as the basisternum, judging from my limited dried material (Fig. 19).

Even if the prosternum of *Z. horningi* presents the most plesiomorphic condition present in Zaleinae, it is probable that the presternum in the groundplan of the subfamily has undergone some broadening relative to that of other canacid groups.

The basisternum in the great majority of taxa included in the Chloropoidea (sensu Colless & D. McAlpine, 1991) is connected to the propleuron on each side by a sclerotized cuticular band, the precoxal bridge. The taxa of Milichiidae, however, are variable in this respect, as some have the
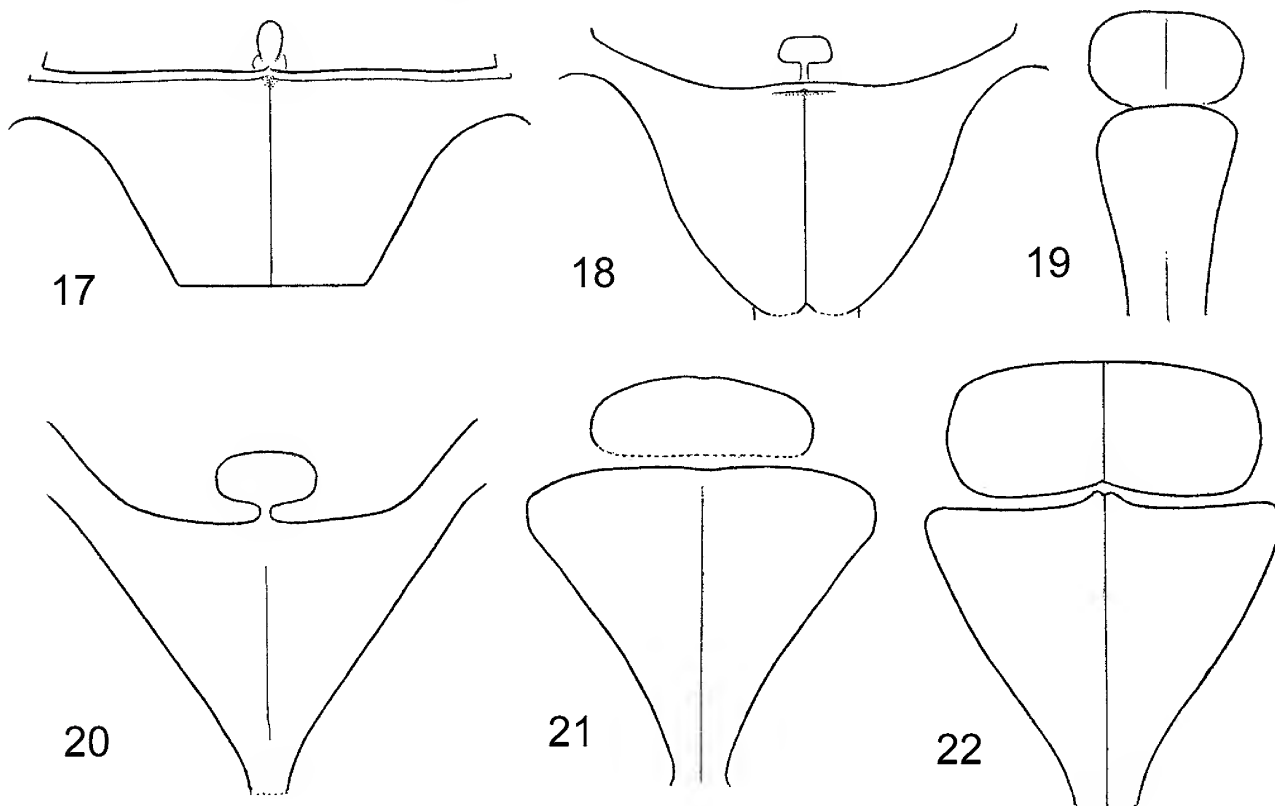
Figs 17–22. Prosternal sclerites of: (*17*) *Apotropina* sp; (*18*) *Tethina pallidiseta*; (*19*) *Suffomyia sabroskyi* n.sp.; (*20*) *Zalea horningi*; (*21*) *Zalea* sp. 1; (*22*) *Z. major*.
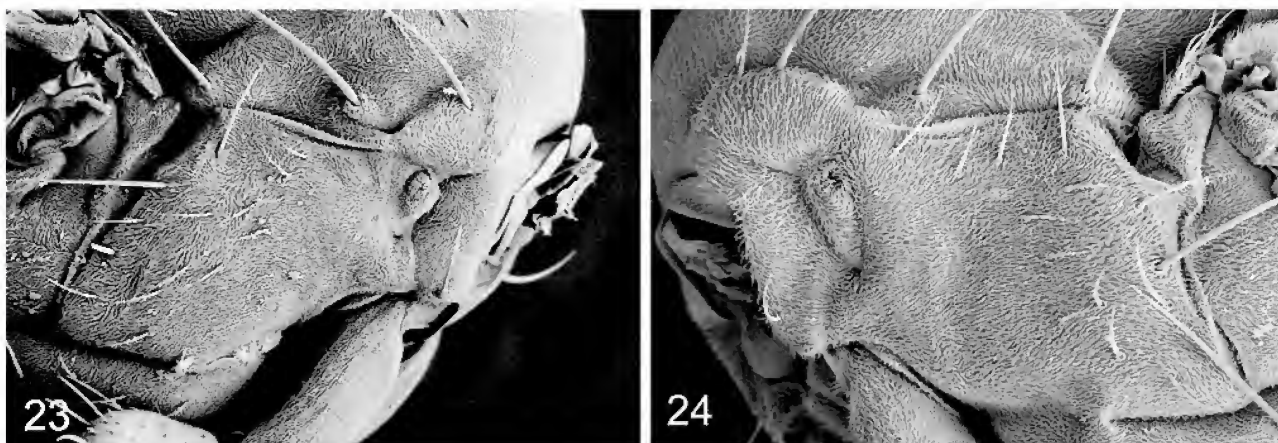
Figs 23, 24. (*23*) *Tethinosoma fulvifrons*, right mesopleuron and adjacent parts. (*24*) *Zalea johnsi*, left propleuron and mesopleuron.

prosternum unbridged and completely separated from the propleuron on each side by a membranous zone. The only examples of Canacidae *s.l.* known to me with the latter condition are included in the Zaleinae. It is clear from the pattern of occurrence of the precoxal bridge, that it must have evolved several times in the Schizophora. Very probably its presence is a groundplan condition of the Chloropoidea, but it is uncertain if it is an autapomorphy for this taxon. The Carnidae *s.l.*, which are hypothesized to be the sister group to the Chloropoidea (in approximately my sense) by J. McAlpine (1989), consistently have the prosternum unbridged.

I originally described the genus "*Zale*" as having the prothoracic precoxal bridge "desclerotised". Freidberg (1995, table 1) gave the precoxal bridge as "reduced" in *Zalea* and "absent" in *Suffomyia*. My detailed studies of many specimens of the Australian *Zalea* spp., including fresh specimens, dried specimens with head removed, and alcohol specimens, show that in all these there is no precoxal bridge, the well sclerotized median plate of the prosternum (basisternum) being isolated from the propleuron by a wide membranous zone on each side (see Figs 16, 22). The condition is thus similar to that in the three known *Suffomyia* spp. However several New Zealand species, including *Z. horningi* and *Z. johnsi* (but not *Z. wisei*), have a distinctly sclerotized precoxal bridge connecting each side of the basisternum to the propleuron (see Figs 15, 20).

This very limited occurrence of the precoxal bridge in Zaleinae raises the question as to whether its possible loss in the groundplan of the subfamily has been reversed for the seven species of the *Zalea horningi* group, which could be monophyletic, or whether this group alone retains the general chloropoid condition, lost in all other zaleine taxa.

The paired subcoxal sclerites, present in many cyclorrhaphous taxa between each fore-coxal base and the basisternum, are not distinguishable in taxa treated in this paper.

Mesopleural chaetotaxy. The mesopleuron or anepisternite of the Canacidae *s.l.* shows a characteristic bristle pattern which is present in some or all constituent taxa of each of the six subfamilies (see Figs 23, 24). There are one or two posteriorly directed bristles very near the central part of the posterior margin, and an upwardly directed bristle near the posterodorsal angle of the sclerite, which is smaller than the largest of the posterior bristles. In addition there is a number of more or less scattered setulae, the majority of which are posteriorly directed, but those on the upper part of the sclerite are directed upwards.

This arrangement of posteriorly directed and upwardly directed bristles is taken as a groundplan condition of the Canacidae *s.l.*, and is absent in the related families Chloropidae and Milichiidae. In the carnid subfamily Carninae (e.g., *Hemeromyia* Coquillett and *Meoneura* Rondani) there is a similar arrangement of major mesopleural bristles with the addition of a large lower mesopleural. If the Carnidae are a closely related outgroup to the Chloropoidea, then it is just possible that the mesopleural chaetotaxy should be considered as a homologous condition in the two groups. The carnid subfamily Australimyzinae (given family rank by J. McAlpine, 1989, but as the probable sister group of Carnidae) has a bare mesopleuron, as has also the genus *Neomeoneurites* Hennig, which is perhaps closer to the Carninae (see Wheeler, 1994). Therefore there must be considerable doubt as to whether the mesopleural chaetotaxy of typical Carninae is anything but a special derived condition, on the basis of comparison with two stepped outgroups. Also I maintain my view that the Carnidae do not otherwise share sufficiently distinctive apomorphies with the Chloropoidea to support the hypothesis of close relationship.

On this basis, I consider that the pattern of mesopleural chaetotaxy in the Canacidae *s.l.* represents a probable autapomorphy for the family.

Tarsal structure. In *Suffomyia scutellaris* (see Freidberg, 1995), *Zalea johnsi* (Fig. 25), and *Z. minor* (Fig. 26) some of the longer ventral setulae on the fore basitarsus are shortly bifid apically. Because this condition can usually only be confirmed by SEM study, I am uncertain of its distribution, but I suspect that it is the general condition for the genus *Zalea*. SEM study shows it to be absent in other canacid genera examined, viz. *Dasyrhicnoessa*, *Pseudorhicnoessa*, *Tethina*, *Pelomyia*, *Tethinosoma*, *Apetaenus* (Fig. 29), *Isocanace*, and *Nocticanace*. Available evidence seems to indicate that presence of bifid basitarsal setulae may be restricted to the Zaleinae, and, because it occurs in at least some species of each probably monophyletic genus, it is probably an autapomorphy for this subfamily.

In *Apetaenus* and some taxa of Canacinae *s.l.* the terminal tarsomere has the dorsal median terminal bristle on a broad prominence and the terminal margin excavated on each
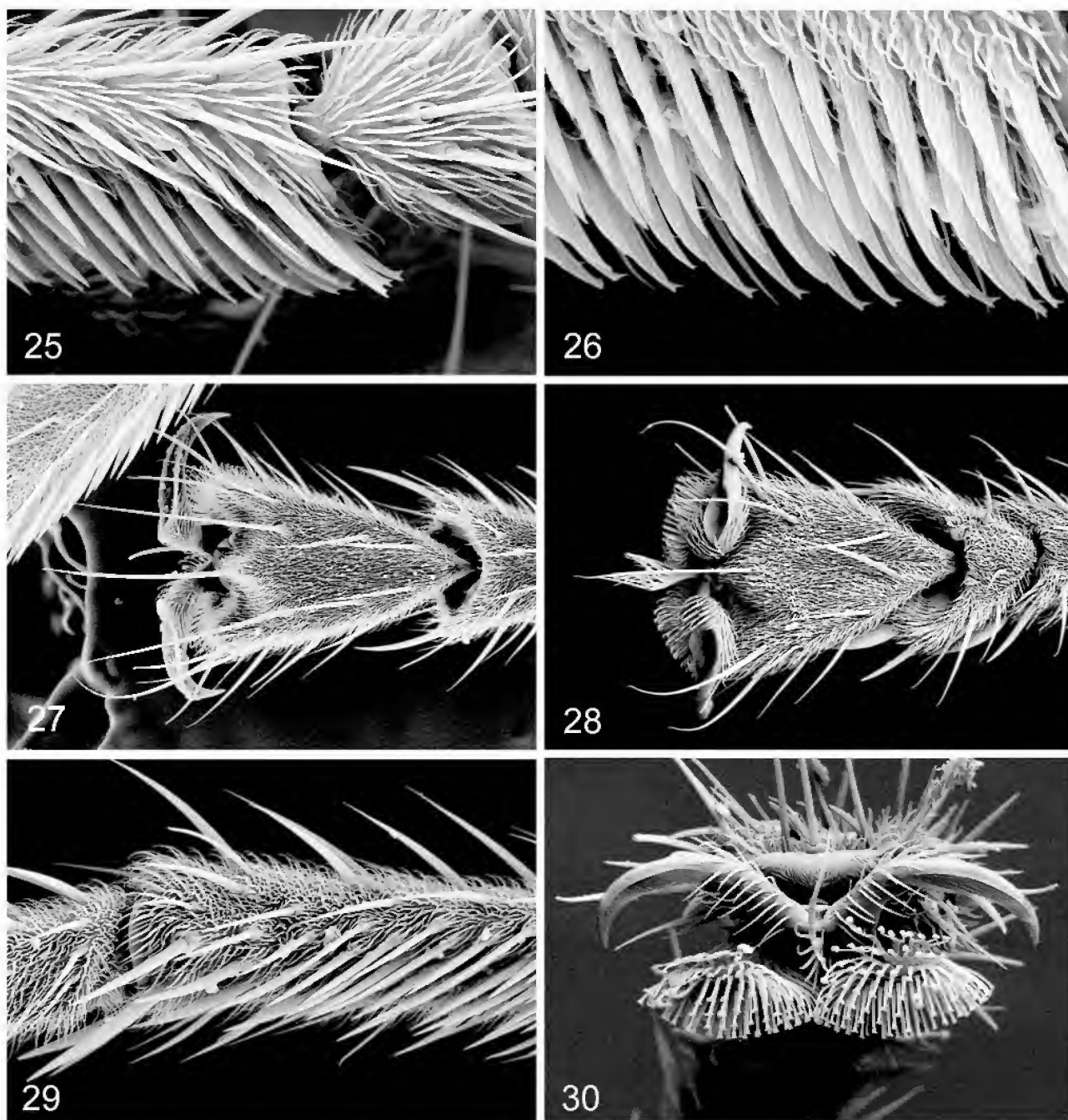
Figs 25–30. (*25*) *Zalea johnsi*, distal part of fore basitarsus. (*26*) *Z. minor*, setulae on ventral surface of fore basitarsus. (*27*) *Apetaenus (Macrocanace) australis*, terminal tarsomere, dorsal view. (*28*) *Nocticanace arnaudi* Wirth, the same. (*29*) *Apetaenus (Macrocanace) australis*, distal part of fore basitarsus. (*30*) *Tethina nigriseta* Malloch, claws and associated structures.

side (Figs 27, 28). In the Zaleinae there is no such median setiferous prominence, but the terminal margin may be slightly excavated.

Pretarsal structures. Pretarsal structures, including especially the claw and empodium, show morphological variation which suggests significant taxonomic characters in the Chloropoidea, but they have been little studied to date. Only limited information can be obtained with the SLM, and as yet I have had limited time and opportunity for work with the SEM.

In the tethinine genera *Dasyrhicnoessa, Pseudorhicnoessa, Tethina,* and *Thitena* the empodium has a slender shaft with well-developed lateral branches. A similar empodium exists in the canacine genera *Canace* Haliday and *Nocticanace* Malloch. In *Pelomyia* the empodium has well-developed lateral and ventral branches (Fig. 34). In *Apetaenus litoralis* Eaton, *A. australis* (Hutton) (Fig. 36), *Neopelomyia*, and *Horaismoptera* the well-developed empodium appears to be simple, unless there are branches near the base that are not easily seen. *Tethinosoma* (Fig. 32) has apparently two unequal lateral branches from near the base of the empodium. In *Zalea minor* the empodium has well-developed lateral branches which are absent on the distal third (Fig. 33). In *Suffomyia ismayi* the branches are restricted to c. the basal third; the more distal branches are
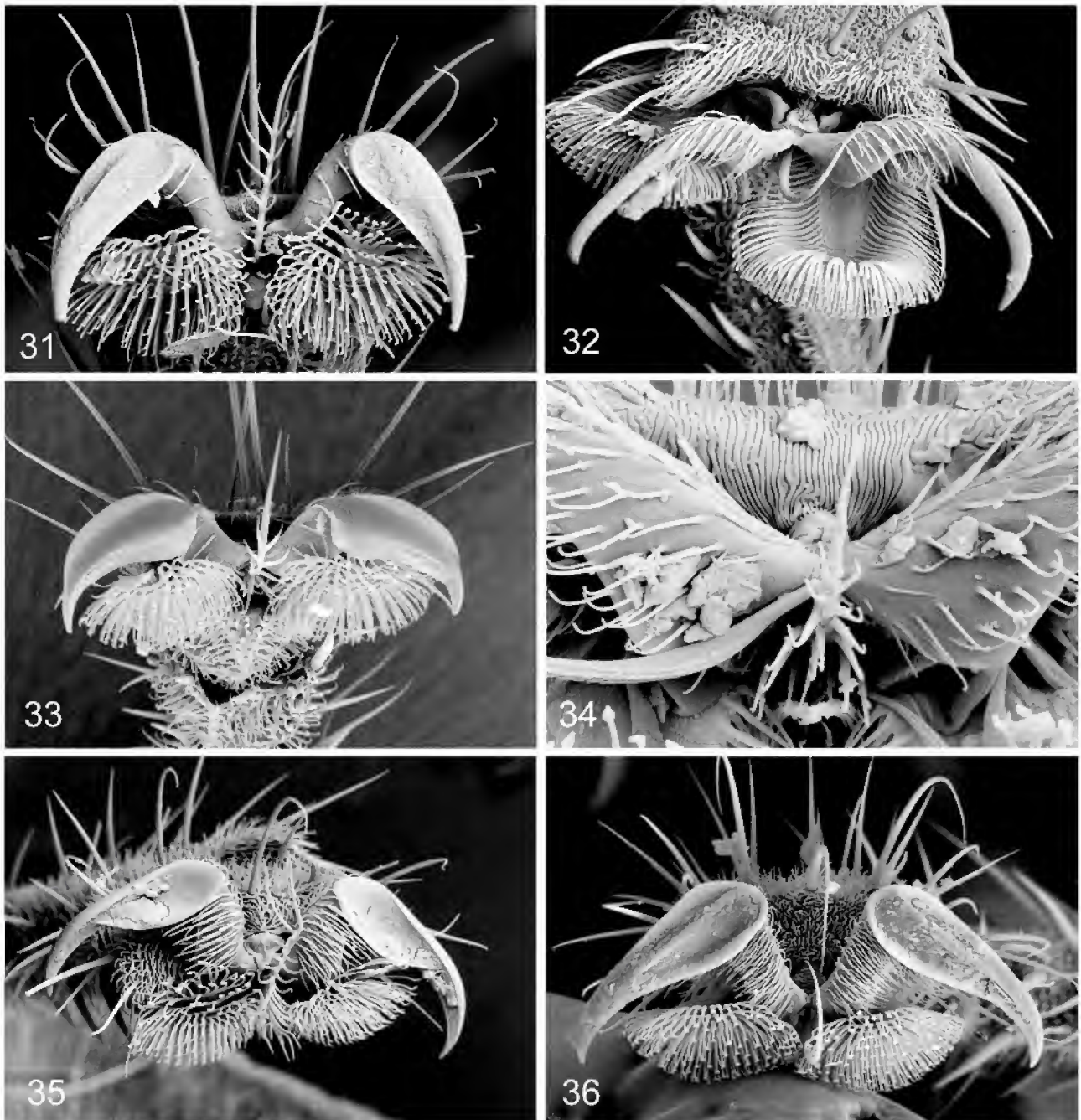
Figs 31–36. (*31*) *Dasyrhicnoessa* sp., claws and associated structures. (*32*) *Tethinosoma fulvifrons*, the same. (*33*) *Zalea minor*, the same. (*34*) *Pelomyia coronata* (Loew), empodium and bases of claws. (*35*) *Nocticanace arnaudi*, claws and associated structures. (*36*) *Apetaenus (Macrocanace) australis*, the same.

much longer than in *Z. minor*, but those near the base become progressively much shorter (CLM in glycerol). It cannot yet be stated whether these characters provide a generic difference between *Zalea* and *Suffomyia*.

The claw in *Tethina* (Fig. 30) is elongate, falcate, and slightly broadened near base, with a pair of weak longitudinal ridges on distal surface. In *Tethinosoma* (Fig. 32) and *Pelomyia* (Fig. 34) the essential structure is very similar. The claw of these taxa does not show a differentiation into basal shaft and distal falx (as defined by D. McAlpine, 1991). In *Dasyrhicnoessa* (Fig. 31) and *Zalea* (Fig. 33) the distal part of the claw (falx) is set apart from the basal part (shaft) in being broadened with a somewhat explanate inner

surface bearing a narrow to quite broad longitudinal ridge but no microtrichia. The claw of *Suffomyia ismayi*, viewed under higher magnification of CLM, is uniformly slender and falcate, with basal ventral tubercle and finely pointed apex; there is no differentiation into shaft and falx. The claw of *Suffomyia sabroskyi*, viewed only with SLM, appears essentially similar to that of *Zalea minor*, but the apex is more finely acuminate. It is thus very different from the claw of *S. ismayi*. Freidberg (1995) states for *S. scutellaris*: "claws widened and flattened centrally". Claws studied of *Nocticanace* and *Isocanace* (subfamily Canacinae *s.l.*) are complex with some of the attributes of *Dasyrhicnoessa*.

Comparison with the outgroup Chloropidae (e.g.,
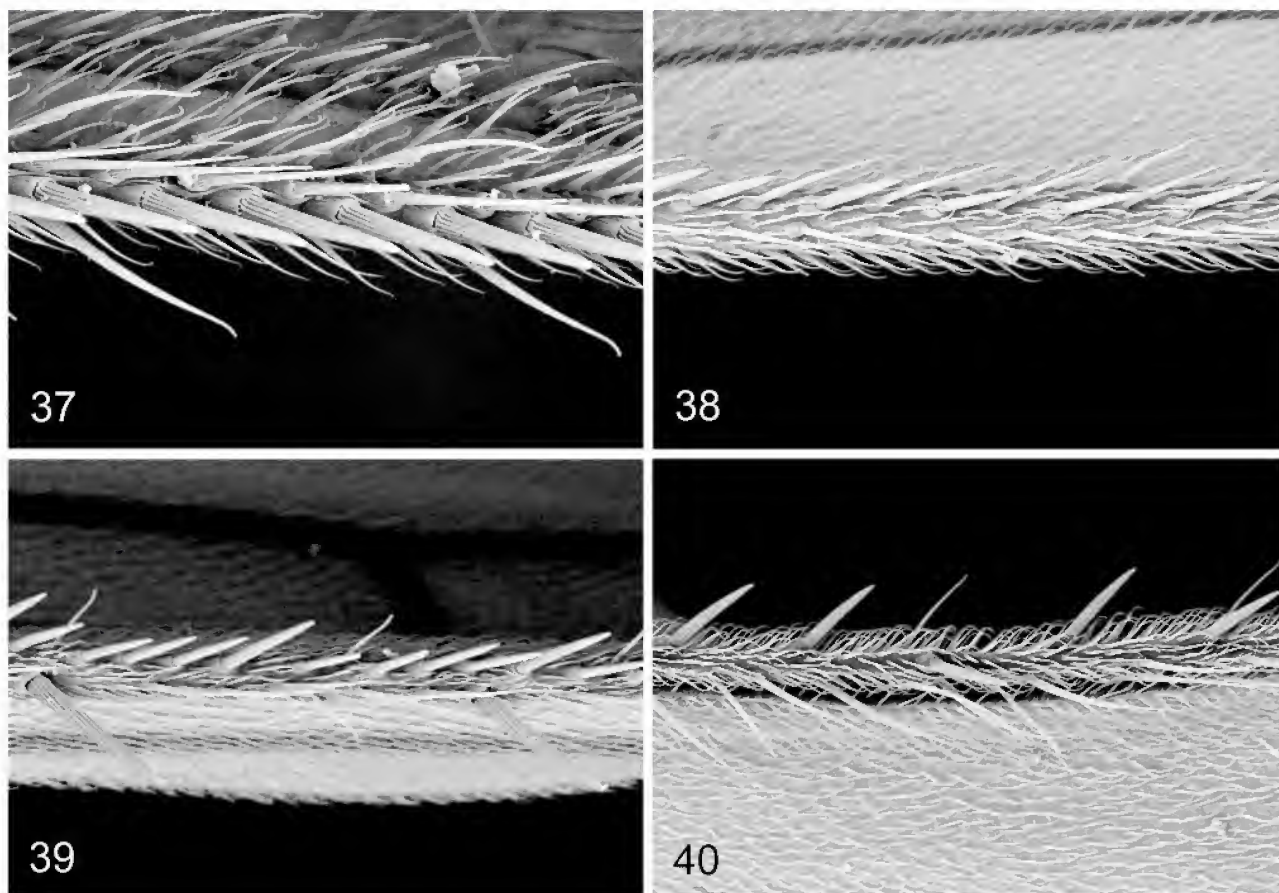
Figs 37–40. (*37*) *Dasyrhicnoessa* sp., part of costa of left wing beyond end of vein 1. (*38*) *Zalea dayi*, the same. (*39*) *Tethinosoma fulvifrons*, the same. (*40*) *Apetaenus (Macrocanace) australis*, the same.

Apotropina sp. and *Cadrema* sp., my studies with SEM) suggests that the relatively simple claw type as in *Pelomyia* and *Tethinosoma* may be nearest the groundplan condition for Chloropoidea, that *Dasyrhicnoessa* and *Zalea* have a more derived claw type, and that the claw type of *Suffomyia ismayi* may be the result of reversal. This hypothesis needs testing from study of a greater range of taxa, preferably with SEM.

Costal chaetotaxy. The arrangement of the different categories of macrotrichium (sensu D. McAlpine, 1973) shows significant taxonomic variation in the Canacidae *s.l.* I attempt to use the terminology of Hackman & Väisänen (1985) both for the different kinds of macrotrichia and for their arrangement patterns, particularly for those on the section of the costa bordering the marginal cell (between veins 1 and 2).

The Tethininae (e.g., *Dasyrhicnoessa*, Fig. 37, *Pseudo-rhicnoessa*, and *Tethina*) have, in addition to seriate hairs and bristles, an anteroventral series of regular, closely placed spinules. This arrangement should comply with the description of type B2 by Hackman *et al.*, but they categorize the Tethinidae under group B1 which should have costal macrotrichia of uniform type. In *Pelomyia* and *Pelomyiella* the spinules are more weakly developed, especially in the latter, though they still form a regular series.

Tethinosoma and *Horaismoptera* differ from other canacids (*s.l.*) in that the section of the costa on marginal cell bears a relatively small number of large widely spaced spines, but the pattern is slightly different in the two genera.

The costa of *Tethinosoma* (Fig. 39) has an irregular series of anterodorsal spinules, and a series of short anteroventral hairs, in addition to non-seriate microtrichia; there are widely space anterodorsal spines, but these are much smaller and more irregular in size and placement than the prominent anteroventral spines. *Horaismoptera* differs in having the anterodorsal spinules stronger and more regularly placed, and the anterodorsal spines much larger than the antero-ventral ones. Also, *Horaismoptera* has a very large costal spine immediately preceding the subcostal break, and an even longer spine preceding the humeral break. Both the humeral break and the associated spine are absent in other taxa of Canacidae *s.l.*

In *Zalea* (Fig. 38) and *Suffomyia* the costa has a series of anterior spinules, which are interspersed with more numerous hairs or short bristles. The spinules are thus more widely spaced than in the Tethininae. Even in the smallest zaleine species, *Suffomyia ismayi*, I find these spaced spinules to be well differentiated, c. 17 being present on the section of costa along the marginal cell.

Apetaenus (Macrocanace) australis (Hutton) (Fig. 40) has a series of anterodorsal costal spines on the marginal cell, but these are much smaller and less spaced than in *Horaismoptera*. In *A. (M.) littoreus* (Hutton) these spines are less developed.

In the Canacinae *s.l.* the arrangement of costal spinules varies. Often they are interspersed with hairs as in the Zaleinae (e.g., in *Isocanace* Mathis), or they may be in two series (e.g., in *Xanthocanace* Hendel and *Procanace* Hendel).
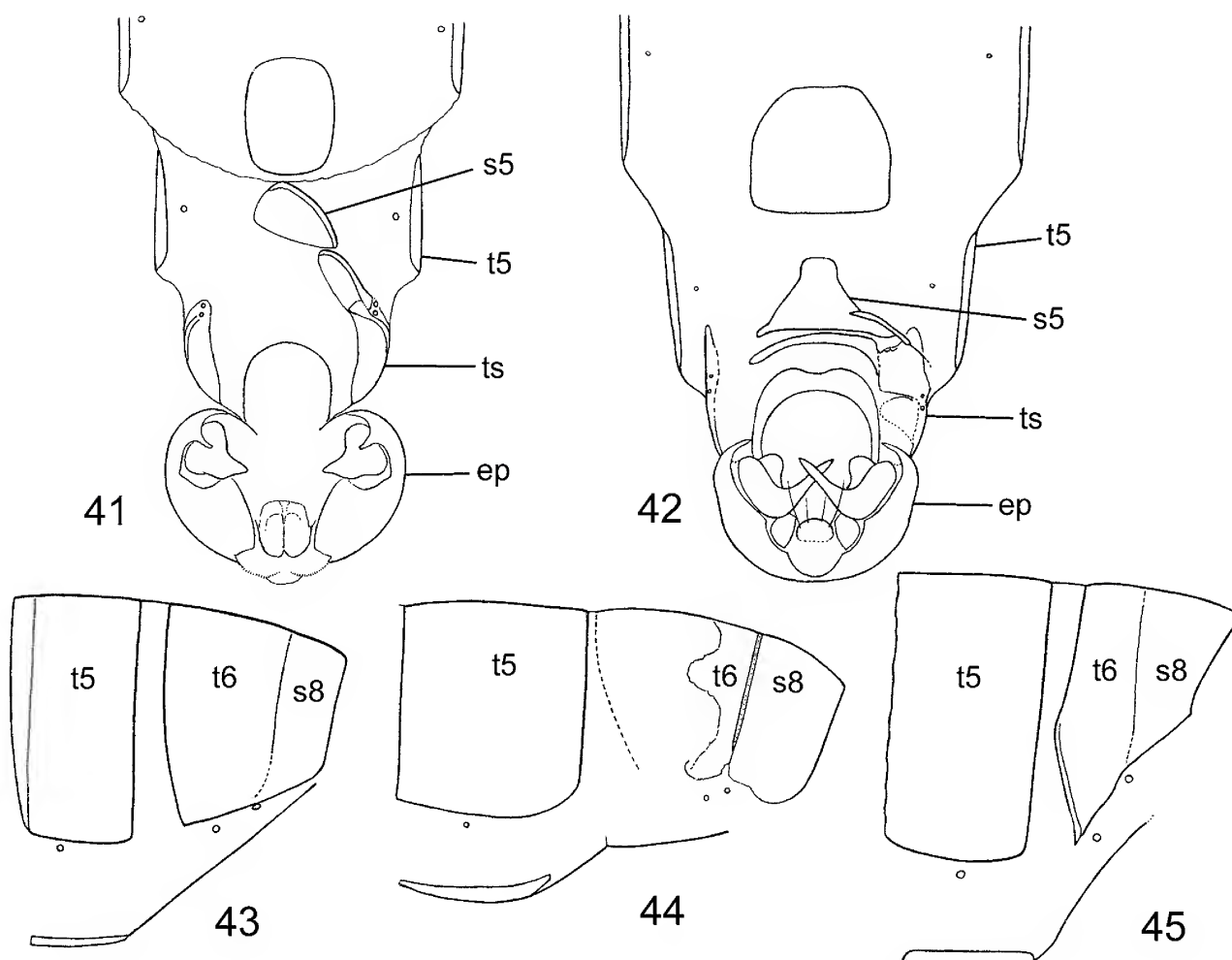
Figs 41–45. (*41*) *Apotropina* sp., male postabdomen, ventral view, hypandrium and associated parts omitted. (*42*) *Siphonellopsis lacteibasis* Strobl, the same. (*43*) *Zalea major*, segment 5 and protandrium. (*44*) *Tethinosoma fulvifrons*, the same. (*45*) *Pseudorhicnoessa* sp., the same; *ep*, epandrium; *s5, s8*, sternites 5 and 8; *t5, t6*, tergites 5 and 6; *ts*, fused tergite 6 and sternite 8.

The veins of the anal region. In the Chloropoidea the veins of the anal region are reduced, by comparison with those of such superfamilies as Sciomyzoidea and Tephritoidea. In the groundplan of the Chloropidae the venation of this part is especially reduced but the probable groundplan condition of the superfamily is indicated by study of the other included families. The anal cell (cup or CuP) is enclosed, but small and compact. Its posterodistal angle probably gives rise only to a very short, stump-like sclerotized vein (vein 6 or CuA_2+A_1), as in Canacinae *s.l.* and Tethininae. Vein 7 (A_2 or 2A) is visible as a curved crease in the membrane with little or no pigment or sclerotization, and does not reach the wing margin. The Carnidae do not agree with this pattern in that their groundplan (as indicated by *Hemeromyia* and *Neomeoneurites*) includes a well sclerotized distal section of vein 6, which is more posteriorly directed than that of any canacid (*s.l.*), and no visible trace of vein 7. In these points they more closely resemble the Odiniidae, Agromyzidae, and Clusiidae.

The groundplan of the Canacidae *s.l.* agrees with that of the Chloropoidea in the above character states. An apomorphy of the Zaleinae (probable autapomorphy for

the subfamily) is the absence of sclerotization of the anal crossvein (transverse section of vein CuA_2 or CuA), which leaves the anal cell open distally. Although the distal section of vein 6 is vestigial in the groundplan of the superfamily, as typified by the Canacinae *s.l.*, Zaleinae, and Tethininae, in the other canacid subfamilies there is a visible crease of variable length in the membrane beyond the anal cell, which appears to follow the old course of vein 6. In the Pelomyiinae the anal crease is rather short but rendered visible by a tract of denser microtrichia. In the Apetaeninae (macropterous forms) and the Horaismopterinae the anal crease is better developed and may reach the wing margin, for example, in *Horaismoptera* and subgenus *Macrocanace*. In *Horaismoptera* the crease is distinctly separated from the anal cell at its base. There is no such separation in *Macrocanace* where the crease is pigmented and looks rather like a genuine vein. However, it is much less sclerotized and less distinctly tubular than all other veins.

I regard the anal crease in the last three subfamilies as probably a secondary development, but I am not convinced that it is a synapomorphy for the three taxa.

Microtrichiation of wing membrane. The Canacidae *s.l.* have generally finer and much denser microtrichiation of the wing membrane than in the probably related families Chloropidae and Milichiidae. This condition is particularly developed in Apetaeninae (macropterous forms), the Canacidae *s.l.*, and the Zaleinae, and is less marked in the Tethininae, especially in *Dasyrhicnoessa*. In the Milichiidae, *Leptometopa* Becker approaches the canacid condition more closely than do other available genera. In the chloropid genus *Apotropina* Hendel, the dune-living *A. exquisita* (Malloch) has fine, dense, canacid-like microtrichiation, but the forest-living *A. nudiseta* (Becker) has very different coarse, spaced microtrichiation as in many other chloropid genera.

The correlation of fine, dense wing microtrichiation with sandy habitat may prove significant in some groups, but I do not find it to be consistent. In the Coelopidae, similarly-sized adults of *Baeopterus philpotti* (Malloch), *Chaetocoelopa sydneyensis* (Schiner), *Coelopa frigida* (Fabricius), and *Gluma musgravei* D. McAlpine all have coarser, less dense microtrichiation than that of *Rhis whitleyi* D. McAlpine. *Rhis whitleyi* is the only one of these species known to burrow actively in sand, and is perhaps more strictly confined to beach habitats in the adult stage. There seems to be a parallel here with *Apotropina* spp. By contrast, among the Canacinae *s.l.*, *Xanthocanace nigrifrons* Malloch, which lives on tidal sand-flats, has markedly coarser, less dense microtrichiation than *Noticanace australis* Mathis, which inhabits rock pools.

The general presence of the fine, dense form of microtrichiation on the wings of canacids probably indicates that it is a groundplan condition for the family Canacidae *s.l.* The fact, that in the outgroups Chloropidae and Milichiidae this condition occurs in only a few, probably more derived taxa, probably indicates that the condition is an autapomorphy for the Canacidae *s.l.*, although the degree of its manifestation in the component taxa is a little variable.

The protandrial sclerites. Following Crampton (1942: 78) I use the term protandrium for the complex of segments between the preabdomen and the genital (ninth) segment in male Cyclorrhapha. In the Schizophora the term is best standardized to mean segments 6 to 8 of the male abdomen inclusively. Through misunderstanding, a particular sclerite in this region has sometimes been termed "protandrium".

In the groundplan of the Schizophora the sclerites of the protandrium have a very asymmetrical arrangement (Crampton, 1942), probably approximated by some modern Coelopidae (D. McAlpine, 1991: fig. 30). However, there are in the Schizophora many reduction series apparent in protandrial morphology and many of these have led to approximate or complete symmetry of the remaining sclerites.

In all but the most derived cyclorrhaphans, a large dorsal sclerite of the protandrium immediately in front of the genital segment is considered to represent the inverted sternite 8 (Crampton, 1942; Griffiths, 1972). However, J. McAlpine (1981) stated: "Also, sternite 7, tergite 8, and sternite 8 usually become more or less fused into a single syntergosternite that occupies a more or less dorsal position". Following this interpretation, many subsequent chapters in that manual (e.g., Vockeroth, 1987) designate this dorsal sclerite as syntergosternite 7 + 8. My own comparative studies of the protandrial sclerites in numerous schizophoran families (e.g., D. McAlpine, 1985b, 1988, 1991) reveal no evidence that this dorsal sclerite generally incorporates tergite 8, which has probably generally been lost by desclerotization. Incorporation of sternite 7 in the dorsal sclerite has probably occurred in some lineages (see numerous diagrams in D. McAlpine, 1985b), but in many schizophoran taxa sternite 7 is only narrowly attached to sternite 8 or is quite separate. I do not therefore accept as a generalization for the Schizophora that sternite 7 forms part of this dorsal sclerite, and I continue the designation as sternite 8, except in those taxa where actual evidence for the compound nature of this sclerite is available.

In those families considered to constitute the superfamily Chloropoidea (sensu Colless & D. McAlpine, 1991, which includes families Chloropidae, Tethinidae, Canacidae, and possibly Milichiidae, but excludes the Carnidae) the only dorsal sclerite of the protandrium appears to be compounded of tergite 6 and sternite 8, on the evidence of (*a*) the presence of a visible trace of a transverse suture often accompanied by difference in texture between the usually short anterior and larger posterior parts of the sclerite; (*b*) the absence of any other sclerite conceivably representing tergite 6; and (*c*) the presence of two pairs of spiracles near its lateral margins (either in pleural membrane below margins of sclerite, or enclosed in sclerite). I treat this condition as a probable autapomorphy for the Chloropoidea. The condition has not been attained in the groundplan of Carnidae which, for this and other reasons, are excluded from the superfamily.

The inclusion of the Milichiidae in the Chloropoidea is ambiguous as it shows variation in some of the supposedly diagnostic characters, but the venation in the anal region of the wing is more like that of the Canacidae than that of the Carnidae. There is the well known modification of the spermathecae shared by the Chloropidae and Milichiidae sometimes considered to be a synapomorphy, but not by J. McAlpine (1989). Any attempt to associate the Acartophthalmidae with the Chloropoidea is likely to be erroneous in view of the complex and fundamental differences in venation, which include both plesiomorphic and apomorphic conditions in this family. Venational characters in the Schizophora are generally among the more stable characters, compared particularly with those of the male postabdomen, and possibly those of the spermathecae.

The most complete and plesiomorphic disposition of protandrial sclerites found in the Chloropoidea is apparently that occurring in certain taxa of the chloropid subfamily Siphonellopsinae, e.g., *Apotropina* Hendel, *Siphonellopsis* Strobl (Figs 41 and 42, see also Nartshuk, 1987: pl. 20). In these flies the protandrium is asymmetrical because of the positions of sternite 6 and the more reduced sternite 7, and the shape of sternite 5 is also asymmetrical. Most chloropid taxa of other subfamilies probably have segment 5 and the protandrium externally symmetrical or almost so. A species perhaps referable to *Psilacrum* Becker (subfamily Oscinellinae) is intermediate, having segment 5 symmetrical and no distinct sclerites representing sternites 6 and 7, but the compound dorsal protandrial sclerite is asymmetrical and much extended on to the pleural region on the left side. This condition is presumed to indicate that a vestige of sternite 7 and perhaps also of sternite 6 has become merged with the lateral margin of the dorsal sclerite. In *Batrachomyia nigritarsis* Skuse (subfamily Oscinellinae, author's observations) the dorsal sclerite is symmetrical,

with no sclerotization extending below the spiracles on either side, a condition indicating the elimination of the laterally placed sternite vestiges. Such a dorsal sclerite is deemed to consist of tergite 6 and sternite 8 only.

Zalea has the dorsal protandrial sclerite large, symmetrical, and evidently compound, (Fig. 43) much as in *Batrachomyia*. This is also the case in typical Canacinae *s.l.* (see Griffiths, 1972).

The Tethinidae have been characterized as having the protandrium symmetrical (Griffiths, 1972; Vockeroth, 1987), with the dorsal sclerite short (D. McAlpine, 1982; Munari, 1999). With further study of tethinid taxa, I no longer consider either condition to be either invariably present or present in the groundplan of the Tethinidae (in so far as a probably paraphyletic group can have a groundplan). The dorsal sclerite is asymmetrical in *Tethina nigriseta* Malloch, being distinctly produced downwards on the left side. Thus it resembles to some extent that of ?*Psilacrum* sp. mentioned above in apparently retaining evidence of sternite 7 merged with the dorsal sclerite. In *Tethina pallidiseta* Malloch this asymmetry is very slight, though discernible in well cleared specimens. Reduction in size of the tergite 6 component of the compound sclerite is evident in these tethinine taxa examined, including *Pseudorhicnoessa* (Fig. 45).

It thus appears that in the groundplan of Canacidae *s.l.* the relatively short tergite 6 is fused to the larger sternite 8, to which a vestige of sternite 7 is fused on the left side. In the Canacinae *s.l.*, in *Masoniella* Vockeroth (see Vockeroth, 1987: figs 13, 14), and particularly in the Zaleinae (Fig. 43), tergite 6 is much larger in proportion to sternite 8. In *Tethinosoma fulvifrons* (Fig. 44) it shows evidence of late reduction from a relatively large sclerite by anterior desclerotization.

Small, often symmetrically placed sclerites on the ventral surface of the protandrium of Canacidae *s.l.*, including some zaleines, (see Papp, 1983: fig. 2; Griffiths, 1972: fig. 147) are probably secondary and not to be identified with particular sternites, from what is known of the reduction stages of these sternites.

The larval cuticle. The larvae remain undescribed for a majority of subfamilies of Canacidae *s.l.*, but are known for a few species of Apetaeninae and Canacinae *s.l.* (Ferrar, 1988, under Coelopidae and Canacidae; Womersley, 1937, under Phycodromidae). In *Procanace* Hendel, *Canaceoides* Cresson, and *Apetaenus* (including *Listriomastax*) a considerable area of cuticle in instar III is densely covered with processes, variously described as spicules, spines, scales, or sclerotized plates. These are quite distinct from the spinose of spiculose segmental creeping pads present in the majority of schizophoran taxa, but the little that is recorded of other tethinid-canacid larvae suggests that they may not be uniformly present in these larvae. Such processes are of infrequent occurrence among acalyptrate taxa, but somewhat similar, often finer processes occur in some taxa of Ephydridae, Periscelididae, etc. where they have almost certainly arisen independently.

If, as appears probable, the cuticular processes are homologous in Apetaeninae and Canacinae *s.l.*, then their presence is probably a synapomorphy indicating relationship between these groups but not necessarily, on my present understanding, excluding other "tethinid" subfamilies from this alliance.

Classification

I have previously placed the Canacidae and Tethinidae in the superfamily Chloropoidea (see D. McAlpine, 1982; Colless & D. McAlpine, 1991). The Chloropoidea included the families Tethinidae, Canacidae, ?Milichiidae, and Chloropidae. Any broader superfamily concept is, I believe, very difficult to justify on the basis of conceived autapomorphies. The evidence for monophyly of the superfamily Carnoidea as constituted by J. McAlpine (1989) is unconvincing. I find no more evidence for synapomorphy between Carnidae and Chloropoidea (sensu Colless & D. McAlpine, 1991) than between Carnidae and Odiniidae-Agromyzidae.

Since I established the subfamily Zaleinae (D. McAlpine, 1982, 1985), doubtfully referring it to the Canacidae, the problem of its systematic position has been mentioned by several authors, for example, J. McAlpine (1989), Mathis (1989), Freidberg (1995). These authors did not offer a resolution to the problem, but considered the Zaleinae to be intermediate between the families Tethinidae and Canacidae, a view that is not phylogenetically meaningful. However, Munari (1999) took the step of transferring Zaleinae to the Tethinidae, referring to Freidberg (1995) as his basis for this action; but Freidberg concluded: "The Zaleinae, however, do not sufficiently match the synapomorphies of either the Canacidae or the Tethinidae and, therefore, cannot be assigned with confidence to either of these families as at present characterized". All of the above authors have mentioned the possibility that the families Canacidae and Tethinidae might be united as a single family, but none appears to have made this family-level synonymy.

Griffiths (1972: 258) considered that the structure of the female postabdomen in the Canacidae s.str. was difficult to reconcile with the hypothesis of close relationship between this family and the Tethinidae. He pointed particularly to the elongation of segments 7 and 8 which he thought to be a synapomorphy connecting the Tethininae with the tephritoid families (his prefamily Tephritoinea—a group no longer considered to have phylogenetic coherence). The female postabdomen of the Canacinae *s.l.* (typically as shown by Wirth, 1987: fig. 5) has distinctive apomorphies, but I see no reason why its structure should not have been ultimately derived from a type resembling that of the "tethinid" *Masoniella* (see Vockeroth, 1987: fig. 8). Griffiths (loc. cit.) commented on the resemblance of the female cercus of the heleomyzid genus *Dihoplopyga* Malloch to that of canacids. *Dihoplopyga* is a junior subjective synonym of *Blaesochaetophora* Czerny (D. McAlpine, 1985b), and has features of the wing and protandrium which exclude it from the Chloropoidea. The resemblance in the cercus (see Malloch, 1933: 191) is due to convergence.

Previously (D. McAlpine, 1982) I referred the Zaleinae with doubt to the Canacidae (as distinct from the Tethinidae), because I thought that the condition of the postvertical bristles and the protandrium in both groups involved exclusive synapomorphies. As indicated in the above discussion of these structures, I am no longer of that opinion.

I am now unable to identify any synapomorphy likely to unite all five subfamilies of the Tethinidae, as given by Mathis & Munari (1996) to the exclusion of the Canacidae s.str. For this reason and because of some possible groundplan synapomorphies for Tethinidae and Canacidae s.str. (possible

autapomorphies for Canacidae *s.l.*) and some less decisive cross-resemblances between included taxa, I take the step of synonymizing the Canacidae and Tethinidae n.syn. the former having nomenclatural priority.

The following three character states (discussed separately above) are here hypothesized as autapomorphies for the Canacidae *s.l.*

1 Mesopleuron (anepisternite) with an upwardly directed bristle on dorsal part, in addition to one or more posterior marginal bristles.
2 Wing membrane with unusually fine, dense microtrichiation.
3 Much of cuticle of larva (instar III) with covering of fine spicules.

Within the superfamily Chloropoidea the Canacidae *s.l.* are excluded from the apparent clade Chloropidae + Milichiidae by the presence of a pair of unmodified spermathecae. The latter clade was given by Hennig (1973), but, apparently without knowledge of the spermathecae in Carnidae, he was doubtful about the inclusion of the latter in the Milichiidae. The inclusion of the Risidae and Cryptochetidae in an otherwise similarly constituted clade by J. McAlpine (1989) is rejected by D. McAlpine (2002). *Risa* Becker was transferred to the Ephydridae by Griffiths (1990), and its position therein affirmed by Mathis & Zatwarnicki (1999).

I divide the Canacidae *s.l.* into six subfamilies, all of which have previously been recognized as such, though the Canacinae have generally been given separate family status in modern literature. The other five subfamilies were treated as subfamilies of Tethinidae by Mathis & Munari (1996).

In briefly treating these subfamilies below, I give their apparent autapomorphies, which provide the strongest evidence for monophyly of each, plus apomorphies which are shared with some other canacid taxa. The shared apomorphies are not necessarily to be interpreted as synapomorphies (homologous character states through the taxa mentioned), though some of them may be such. I do not now have the opportunity for a thorough cladistic study of the family.

Subfamily Tethininae Hendel, 1916 (as Tethinidae)

Included genera. *Afrotethina* Munari; *Dasyrhicnoessa* Hendel (including *Sigaloethina* Munari); *Pseudorhicnoessa* Malloch; *Tethina* Haliday (including *Rhicnoessa* Loew); *Thitena* Munari; ?*Plesiotethina* Munari.

Autapomorphy: frontal orbit with a series of proclinate-inclinate setulae.

Shared apomorphies: all fronto-orbital bristles strongly curved outwards (shared with Canacinae); humeral callus with at least two differentiated bristles (shared with Horaismopterinae).

Distribution. Most tropical and warm-temperate coasts of the world.

Subfamily Zaleinae D. McAlpine, 1985

syn. Zalinae D. McAlpine, 1982

Included genera. *Zalea* D. McAlpine; *Suffomyia* Freidberg.

Autapomorphies: postvertical bristles more or less divergent; prothoracic presternum broadened; fore basitarsus with some bifurcate ventral setulae; anal crossvein (CuA_2 + A_1) obsolete.

Shared apomorphies: claws differentiated into slender basal shaft and broadened distal falx (shared with *Dasyrhicnoessa*, condition reversed in *Suffomyia ismayi*); in compound protandrial sclerite, area of tergite 6 markedly greater than area of sternite 8 (shared with Canacinae). Possible apomorphy (relative to groundplan of Chloropoidea): eye with well-developed ommatrichia, c. as numerous as ommatidia (shared with some Tethininae).

Distribution. Australasia—tropical to cool temperate; Middle East.

Subfamily Horaismopterinae Sabrosky, 1978

Included genera: *Horaismoptera* Hendel; *Tethinosoma* Malloch.

Autapomorphies: antennae widely divergent from bases; antennal segment 2 with seriate short, stout spines or spinescent setulae on medial surface; one to three inclinate fronto-orbital bristles all situated below eclinate fronto-orbitals; costa with oblique, incised notch at subcostal break; costa, beyond subcostal break, with well spaced series of anterodorsal and anteroventral spines.

Shared apomorphies: distal section of vein 6 long and distinct (shared with Apetaeninae and, to some extent, with Pelomyiinae); humeral callus with at least two differentiated bristles (shared with Tethininae).

Distribution: New Zealand; shores of Indian Ocean; Middle East; Namibia.

Subfamily Apetaeninae Mathis & Munari, 1996

Included genus: *Apetaenus* Eaton. See Mathis & Munari (1996) for bibliographic data and list of species.

Autapomorphies: mid one of three fronto-orbital bristles further from eye than others; costa curved just before subcostal break (apparent only in macropterous forms); facial sclerotization sharply divided by complete median membranous strip (partial desclerotization only in some Tethininae and Zaleinae); area of wing membrane behind vein 6 and distad of alula reduced (apparent only in macropterous forms); syntergite 1 + 2 in female longer than rest of abdomen (condition approached in a few Canacinae).

Shared apomorphies: prelabrum enlarged (shared with Canacinae); terminal tarsomere triangular with median terminal bristle on a tubercle, with broad excavation on each side which forms a depression on dorsal surface (see Fig. 27; this condition approximated in some Canacinae, e.g., *Nocticanace arnaudi* Wirth, Fig. 28); vein 6 long and conspicuous (shared with Horaismopterinae); membranous strip separating tergites 1 and 2 in mid-dorsal region lost (shared with most Canacinae); cercus of female shining, without pruinescence (microtrichia) between setulae or almost so (shared with some Canacinae; cercus extensively pruinescent in all other subfamilies).

Distribution: oceanic islands south of 45°S.

Listriomastax Enderlein was synonymized under *Apetaenus* by Hennig (1971), but Papp (1983) said that these two genera "are not closely related," without giving reasons. *Macrocanace* Tonnoir & Malloch was synonymized under *Apetaenus* by Mathis & Munari (1996).

Macrocanace can be retained as a subgenus of *Apetaenus* to include *A. (Macrocanace) australis* (Hutton) and *A. (Macrocanace) littoreus* (Hutton). The subgenus includes consistently macropterous flies, with a series of long dorsal setulae on vein 1, the humeral bristle relatively large, and the setulae on abdominal tergites relatively short and inconspicuous—all character states contrasting with those of *Apetaenus (Apetaenus) litoralis* Eaton, the type species of *Apetaenus*. I do not have material for deciding if there are grounds for retention of *Listriomastax* as a subgenus. *Apetaenus litoreus* (Enderlein, 1909) is a secondary junior homonym of *Apetaenus littoreus* (Hutton, 1902) under Article 58.7 of ICZN (1999). I prefer not to introduce a replacement name for the former, until I feel assured of the stable congeneric status of the two species.

Subfamily Pelomyiinae Foster, 1976

Included genera: *Pelomyia* Williston; *Pelomyiella* Hendel; *Neopelomyia* Hendel; *Masoniella* Vockeroth. *Neopelomyia* differs from typical genera in facial structure, probably as a specially derived condition in this genus in connection with elongation of the proboscis. *Masoniella* has been placed in the Tethininae, but Foster & Mathis (2003) confirmed its placement in the Pelomyiinae.

Autapomorphies: fore coxa elongate; discal and second basal cells (dm and bm) confluent.

Shared apomorphies: lower margin of face and prelabrum displaced posteriorly on ventral surface of head (condition shared with Horaismopterinae, approached in few Tethininae; condition probably reversed in *Neopelomyia*; condition unknown to me in *Masoniella*); distal section of vein 6 sharply defined (but quite desclerotized and not nearly reaching margin, condition in *Masoniella* unrecorded; this condition much more developed in Horaismopterinae and Apetaeninae).

Distribution: Americas; Palaearctic Region; temperate Australia. Unlike most canacids (*s.l.*), these flies are not restricted to coastal habitats.

Subfamily Canacinae Jones, 1906

Included genera: these were catalogued by Mathis (1992) under subfamilies Canacinae and Nocticanacinae (i.e. Canacidae s.str.). Australian genera were keyed by Mathis (1996).

Autapomorphies: postvertical bristle absent; face prominent, extensively visible in profile; prementum of proboscis very broad, deeply cleft distomedially; cercus of female basally thickened and fused with epiproct, distally with one or two thickened bristles.

Shared apomorphies: fronto-orbital bristles strongly curved outwards (shared with Tethininae); subcranial cavity and anteclypeus enlarged (shared with Apetaeninae); abdominal tergites one and two with intervening membranous strip in mid-dorsal region weakly developed or absent (consistently absent in Apetaeninae); compound dorsal sclerite of protandrium with tergite 6 markedly larger in area than sternite 8 (shared with Zaleinae).

Distribution: mainly tropical and warm temperate coasts of world; few cool temperate records, e.g., British Isles; few species found inland.

Key to subfamilies of Canacidae *s.l.*

1   Frontal orbit with three to five major outwardly inclined bristles, of which foremost is near level of ptilinal fissure, in addition to an inner series of three or more proclinate-inclinate shorter bristles or setulae; proclinate-inclinate interfrontal bristles in two distinct series; pair of convergent, often widely spaced postverticals present; costa along marginal cell with a continuous series of closely placed short black anterior spinules, and no series of longer, widely spaced spines; discal and second basal cells separate; anal cell closed; vein 6 not extending distinctly beyond anal cell, even as a sharp fold in membrane .... Tethininae

—— Fronto-orbital bristles not arranged as above; if biseriate interfrontal bristles present, then either convergent postvertical bristles absent or anal cell open distally; other characters variable 2

2   Face, at least on lower part, almost vertical, not receding on to ventral surface; prelabrum thus located approximately as far forward as anterior surface of head capsule 3

—— Face, in profile, convex below, markedly receding on to ventral surface of head; prelabrum thus markedly displaced posteriorly 5

Neopelomyia, probably referable to Pelomyiinae, disagrees in these characters, but differs from other subfamilies in having discal and second basal cells confluent.

3   Wing either vestigial, or with long vein 6 extending to margin; fronto-orbital bristles normally three, of which middle one is reclinate and further from eye than others; female: syntergite 1 + 2 longer than rest of abdomen .... Apetaeninae

—— Wing unreduced, with vein 6 scarcely extending beyond anal cell; if three fronto-orbital bristles present, then middle one not further from eye than others; syntergite 1 + 2 not normally as long as rest of abdomen 4

4   Anal cell closed; face prominent, extensively visible in profile, entirely sclerotized; prelabrum large and very broad; prementum very broad, deeply cleft distomedially; tergites 1 and 2 without or with quite indistinct weak line of demarcation mid-dorsally; cercus of female basally thickened and fused with epiproct, distally tapered, with one or two spinescent bristles .... Canacinae

—— Anal cell open distally; face not prominent; prelabrum of moderate size, c. half width of surrounding subcranial membrane, and not over one quarter width of head; prementum not much broader than long, nor deeply cleft; tergites 1 and 2 separated in mid-dorsal region by distinct membranous strip, fused at sides; cercus of female basally articulated, distally blunt, without spinescent bristles .... Zaleinae

5   Antennae widely divergent from bases; antennal segment 2 short, collar-like, with series of short, stout spines or spinescent setulae on medial surface; one to three incurved fronto-orbital bristles located below the two upper eclinate fronto-orbitals; upper postocular bristle (behind outer vertical) present; scutellum dorsally setulose; fore coxa broad, less than $\frac{2}{3}$ as long as fore femur; costa with obliquely incised notch at subcostal break, beyond break with a well spaced series each of anterodorsal and anteroventral long spines; discal cell closed basally by well sclerotized vein .... Horaismopterinae

—— Antennae subparallel; antennal segment 2 not remarkably short, with few fine setulae on medial surface; incurved fronto-orbital bristles absent; upper postocular bristle absent; scutellum without setulae; fore coxa elongate, at least $\frac{2}{3}$ as long as femur; costa with simple subcostal break, beyond break without such spaced spines; discal cell basally confluent with second basal cell .... Pelomyiinae

Subfamily Zaleinae

Diagnostic description

Head. Pseudopostocellar bristles absent; postvertical bristles proclinate, usually more or less divergent, at bases at most slightly closer to nearest inner vertical than to each other; fronto-orbital bristles three, all reclinate or posterior one variably curved outwards; vibrissa located either at anterior extremity of cheek (as seen in profile) or distinctly behind this point; facial ridge not prominent, without tubercle; face not prominent, usually nearly vertical, lightly sclerotized except on lower median part; eye with many well-developed ommatrichia, c. as numerous as ommatidial facets. Antennae subparallel, decumbent; segment 2 with any setulae on medial surface inconspicuous or absent; segment 5 usually stout, microtrichose; segment 6 with moderately dense short to moderate hairs. Subcranial area not enlarged; prelabrum well developed but not broad, not set back from anterior surface of head; proboscis of moderate dimensions; prementum longer than wide, not cleft distomedially; labella not posteriorly prolonged.

Thorax. Dorsocentral bristles four pairs; one humeral bristle differentiated; scutellum with two pairs of major bristles, sometimes also with one or two pairs of smaller bristles, but without dorsal setulae; prosternum with presternum at least moderately developed, basisternum with or without precoxal bridge. Costa on marginal cell with a series of anterior spinules interspersed at short intervals among more numerous hairs or short bristles; discal cell separate from second basal cell; anal cell open distally; distal section of vein 6 represented only by indistinct crease in membrane.

Abdomen. Tergites 1 and 2 separated in mid-dorsal region by narrow membranous strip, their combined length much less than that of rest of abdomen. Male: dorsal protandrial sclerite symmetrical (i.e. without visible vestige of sternite 7), remarkably large because of large tergite 6 component; epandrium with at least one pair of basally fully articulated surstyli; hypandrium (so far as known) with at least one comb of three bristles on each side. Female: postabdominal segments very extensile; cercus simple, straight, blunt, basally articulated, without spines.

Key to genera of Zaleinae

1   Postfrons without setulae between anterior ocellus and anterior margin; distal section of subcosta (beyond humeral crossvein) well sclerotized on c. middle third, obsolete and unpigmented on c. distal third, and much weakened towards base; first basal cell not separated from second basal cell by any sclerotized vein; ♂: only one pair of surstyli present; ♀: abdominal tergite 7 without anterior apodeme (♀ unknown in *S. ismayi*) .... *Suffomyia*

——Postfrons with several setulae on central anterior part; distal section of subcosta almost uniformly sclerotized from humeral crossvein to termination at subcostal break of costa; first and second basal cells almost or completely separated by a sclerotized vein; ♂: two pairs of surstyli present; ♀: abdominal tergite 7 with median, posteriorly forked apodeme attached to its anterior margin (Figs 56, 71–74, not yet investigated for *Z. wisei* etc.) .... *Zalea*

Genus *Zalea* D. McAlpine

Zale D. McAlpine, 1982: 108–110. (Preocc. Hübner 1818.) Type species (original designation) *Z. minor* D. McAlpine.
Zalea D. McAlpine, 1985: 82. Replacement name for *Zale* D. McAlpine.

Diagnostic description. Small to very small flies; wing c. 1.4–3.0 mm long. Arista three-segmented; antennal segment 4 distinct but small.

Head. Postvertical bristles proclinate, divergent to convergent; postfrons with several setulae on central part in front of ocelli, often tending to form a double series, like rudimentary interfrontal bristles, also with few smaller setulae on frontal orbits and between ocelli.

Thorax. Prothoracic precoxal bridge present or absent; acrostichal setulae biseriate, extending posteriorly to the distinct prescutellar acrostichal bristle; scutellum with two major bristle pairs and, in most species no other bristles or setulae. Mid femur with distal posteroventral comb of short suberect bristles in male (sometimes blunt and incrassate, always absent in female). Distal section of subcosta almost uniformly sclerotized from humeral crossvein to termination in subcostal break; anterior crossvein meeting vein 4 near or distad of mid-length of discal cell, except in *wisei* group; basal section of vein 4 separating first and second basal cells slender but well sclerotized; alula scarcely narrowed distally, with largely transverse distal margin, with marginal setulae much shorter than maximum width of alula.

Abdomen of male. Dorsal protandrial sclerite c. twice as long as tergite 5 or slightly less; two pairs of basally articulated surstyli present; hypandrium on each side with two combs of three closely placed setulae each, one comb much larger than the other (Fig. 53, setulae of smaller group not yet observed in some species though possibly present); distiphallus subcylindrical, elongate, but not very long, largely membranous, encircled by three prominent papillae (one posterior and two anterior).

Abdomen of female. Tergite 7 with median anterior posteriorly forked apodeme, which is incorporated in floor of pouch below margin of tergite 6 (not investigated for some New Zealand spp.)

Distribution. Australia: temperate coasts, but not yet recorded for Queensland and South Australia. New Zealand: North Island; South Island; Snares Islands.

Notes

The following two apparent autapomorphies, not present, so far as known, in *Suffomyia*, support the monophyletic status of *Zalea*: in male, base of distiphallus encircled by three membranous papillae; in female, tergite 7 with median, anterior, posteriorly forked apodeme. The aedeagal details have not been fully checked for the *wisei* group, but, in the only microscopic preparation of *Z. wisei*, there appear to be structures in the nature of membranous papillae. Although the presence of the internal apodeme is not yet confirmed for females of some New Zealand species, the doubtful species are closely related to better known ones, or others in which the external features of sternite 7 are consistent with the presence of an apodeme (as in the *wisei* group). The complex hypandrium in such diverse species as *Z. johnsi*, *Z. clava*, and *Z. minor* is so uniform and distinct from that of *Suffomyia scutellaris* as figured by Freidberg (1995), that it may provide further cladistic data when a better range of material is available.

The known species of *Zalea* are divisible into three morphologically well defined groups. It is uncertain if these are monophyletic, because of doubt as to the state of certain characters in the groundplan of the genus, e.g., orientation of postvertical bristles, prosternal structure, and presence/absence of certain bristles.

1   *Horningi* group: *Zalea johnsi, Z. mathisi, Z. uda, Z. ohauorae, Z. lithax, Z. horningi, Z. earlyi* (New Zealand).

2   *Wisei* group: *Zalea* sp. 1, *Z. wisei* (New Zealand).

3   *Minor* group: *Zalea clava, Z. minor, Z. major, Z. dayi* (Australia), ?*Zalea* sp. 2 (New Zealand).

These groups are characterized below in the key to species. It is added that the *horningi* group is the only one with bridged prosternum.

Key to species of *Zalea*

1   Scutellum with shorter pair of bristles at apex, in addition to two major pairs; anterior crossvein meeting vein 4 well before mid length of discal cell; posterior fronto-orbital bristle strongly curved outwards, not reclinate, in contrast to other fronto-orbitals; upper postgenal setulae forming an almost vertical series; wing typically over 2.1 mm long; habitat New Zealand .... (*wisei* group) 2

—— Scutellum with two pairs of major bristles only; anterior crossvein meeting vein 4 at or beyond mid-length of discal cell; posterior fronto-orbital bristle reclinate and slightly curved outwards, its orientation not markedly different from mid fronto-orbital; upper postgenal setulae usually absent or little developed (except in *Z. earlyi*); habitat Australia or, if New Zealand, then wing under 2.1 mm long 3

2   Triangle formed from joining centres of ocelli broader than equilateral triangle; antennal segment 5 less than 2.5× as long as wide; palpus not extending anteriorly beyond prelabrum when proboscis is withdrawn; cheek region descending in outline and most prominent posteriorly (Fig. 70) .... *Zalea* sp. 1

—— Triangle formed by joining centres of ocelli not broader than equilateral triangle; antennal segment 5 more than 3.5× as long as wide; palpus extending distinctly beyond prelabrum when proboscis is withdrawn; cheek region not more ventrally prominent posteriorly than anteriorly (Fig. 68) .... *wisei*

3   Prosternum with precoxal bridge on each side (Fig. 15); male (where known): posterior surstylus extensively microtrichose on outer surface; habitat New Zealand .... (*horningi* group) 4

—— Prosternum without precoxal bridge (Fig. 16); male (unknown in sp. 2): posterior surstylus almost devoid of microtrichia; habitat mostly Australia, but see also sp. 2 (northern New Zealand) .... (*minor* group) 10

4   Postgenal setulae forming an almost vertical series; postvertical bristles slightly divergent to subparallel; female: tergite 7 with pair of separate broad lateral plates detached from T-shaped apodeme .... *earlyi*

—— Postgenal setulae absent or little developed; postvertical bristles variable; female (where known): tergite 7 and its anterior apodeme forming a single, lobed sclerite 5

5   Postvertical bristles divergent; male: anterior surstylus much longer than posterior surstylus, strongly curved so that apex is directed posteriorly; posterior surstylus broad, with enlarged anterior setulae near mid-length .... *johnsi*

—— Postvertical bristles convergent or rarely parallel; male: anterior surstylus variable, but usually not markedly longer than posterior surstylus; posterior surstylus without such large anterior setulae 6

In this section, only males are identifiable at present, but South Island and Snares Islands populations studied so far are probably referable to *Z. horningi*.

6   Anterior surstylus much compressed, subspatulate, nearly straight; posterior surstylus subovate, less than 3× as long as width near mid-length, without coarsely setulose sub-basal prominence .... *horningi*

—— Anterior surstylus curved, slender or somewhat distally compressed; posterior surstylus variable 7

7   Posterior surstylus not over c. 2× as long as maximum width 8

—— Posterior surstylus c. 4× as long as width near mid-length 9

8   Anterior surstylus very slender, rod-like, with few small setulae only; posterior surstylus subovate, very oblique basally, broadly rounded apically (Fig. 52) .... *mathisi*

——Anterior surstylus less slender, slightly compressed; its inner surface with numerous stout setulae, some of which are short and subconical; posterior surstylus subtriangular, with basal articulation transverse and apex subacute to narrowly obtuse (Fig. 54) .... *uda*

9   Anterior surstylus with all setulae fine, minute; posterior surstylus apically broadly rounded and compressed, gradually incurved .... *lithax*

——Anterior surstylus with some large setulae on inner surface, those near base relatively stout, distal ones quite long; posterior surstylus subangularly bent inwards near mid length, straight beyond, distally attenuated, its apex as slender as that of anterior surstylus .... *ohauorae*

10   Palpus much swollen distally, where more than half as deep as cheek; fore tibia with one posterodorsal bristle or outstanding setula slightly beyond mid-length, which is at least as long as tibial diameter; mid tibia with similar dorsal bristle near mid-length; female: paired sclerites of sternite 7 broad, separated by much less than width of each; habitat southwestern Australia .... *clava*

——Palpus slightly swollen distally, where less than half as deep as cheek; fore and mid tibiae with no such long dorsal or posterodorsal bristle; female: paired sclerites of sternite 7 narrower and separated by more than width of each; habitat eastern Australia 11

11   Males 12

——Females 14

12   Width of epandrium at least 0.38 mm (even in dried specimens); anterior surstylus broadest at base, markedly tapering from just beyond base; length of wing usually over 2.0 mm .... *major*

——Width of epandrium not over 0.32 mm; anterior surstylus not broadened at base; length of wing usually less than 2.0 mm 13

13   Mid femur with short, thick posteroventral bristles of distal comb all with finely pointed apices; anterior surstylus broad and scoop-like distally; posterior surstylus with finely pointed apex .... *dayi*

——Mid femur with short posteroventral bristles of distal comb mostly very blunt; anterior surstylus rod-like, though distally compressed; posterior surstylus with obtuse apex .... *minor*

14   Abdominal sternites 3, 4, 5 broad, all broader than long; paired sclerites of sternite 7 very narrow, separated by more than four times width of each (Fig. 85) .... *dayi*

——Abdominal sternites 3, 4, 5 narrow; paired sclerites of sternite 7 not attenuated, separated by less than three times width of each (Fig. 84) 15

15   Tergite 6 markedly desclerotized on middle of posterior margin, markedly broader than tergite 5 and encroaching on pleural region on posterolateral angles, sternite 6 medially notched, not divided; tergite 7 divided in two by extensive median desclerotization (Fig. 78), connected only by forked apodeme; length of wing usually over 2.0 mm .... *major*

——Tergite 6 not or only slightly desclerotized on posterior margin, scarcely broader than tergite 5; sternite 6 divided in two; tergite 7 imperfectly divided, sclerotized on almost full width of posterior margin (Fig. 76); length of wing usually less than 1.9 mm .... *minor*
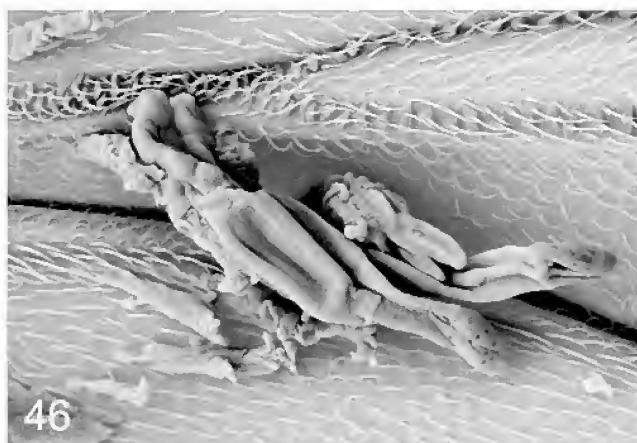
Figs 46, 47. (*46*) fungal ascomata on ventral surface of wing of *Zalea minor*. (*47*) fungal ascomata on hind tibia of *Z. minor*.

Zalea johnsi n.sp.

Figs 15, 24, 25, 48, 50, 51

Material examined. HOLOTYPE ♂, New Zealand (South Island): Kaikoura Peninsula [East Head on some maps], 26–28.i.2000, D.K.M., R.M. (NZAC). Dry-mounted on triangular card. PARATYPES. South Island: 5♂♂, 2♀♀, same data as holotype (AM, CMC, USNM); 6♂♂, 2♀♀, Paratai Point, Kaikoura district, 26–27.i.2000, D.K.M., R.M. (AM, NZAC, ZMC).

Other material. South Island: 2♀♀, Jackson's Bay, near Haast (AM).

Description (♂, ♀). Appearance and habitus resembling those of *Z. minor, Z. horningi*, etc.

Coloration. Head predominantly grey-brown; anterior margin of postfrons narrowly rather yellowish brown; parafacial and much of cheek yellowish with covering of pale grey pruinescence; hypofacial and posterior extremity of cheek darker, greyish. Antenna tawny-brown; segment 3 darker distally than basally; arista blackish. Prelabrum grey-brown; palpus greyish tawny. Thorax with blackish ground colour; mesoscutum and scutellum with brown pruinescence; pleura with grey to greyish brown pruinescence. Legs, including tarsi, dark greyish brown. Wing membrane uniformly smoky grey; veins dark brown. Halter yellow, with pale creamy capitellum. Abdomen dark grey-brown, almost entirely pruinescent; in male, anterior surstylus shining brown, darkest towards base; in female, tergite 7 extensively shining black anteriorly, pruinescent dark grey towards posterior margin; cercus of female brown.

Head and eye both much higher than long; height of cheek c. 0.23–0.27 of height of eye; face almost flat and vertical (when uncollapsed), but recessed between parafacials on upper part; vibrissal region of cheek less anteriorly produced than in *Z. major* and *Z. minor*, so that the moderately short vibrissa is situated almost at its anterior extremity, as seen in profile; postgenal setulae absent; postvertical bristles divergent, much smaller than ocellars and fronto-orbitals. Palpus shorter than in Australian species, slightly widened distally.

Thorax. Prosternum with well sclerotized precoxal bridge; scutellum without setulae, with only the two pairs of major bristles. Mid femur of male with a mostly sparse series of

posteroventral bristles, those just beyond mid-length shorter, slightly thickened, more closely placed, with curved sharp apices, forming ill defined comb; in female posteroventral bristles of mid femur absent or little differentiated from setulae; fore tibia generally with three or more dorsal to posterodorsal setulae or bristles, as long as or longer than tibial diameter; mid and hind tibiae also with some moderately long dorsal setulae or bristles. Wing: cell-4 index = 0.50–0.58.

Abdomen. Sternite 1 divided into two small, widely separated sclerites; sternite 2 without accessory sclerites. Male: epandrium coarsely setulose, without any distinct bristle pairs; anterior surstylus slender, much curved so that slender but compressed apical part is directed posteriorly, with scattered setulae longest on posterior surface of basal half, and with few microtrichia restricted to inner surface near apex; posterior surstylus broad, narrowly rounded at apex, strongly incised posteriorly at base to produce sub-basal prominence, very extensively microtrichose except near anterior margin, outer surface with scattered small setulae and longer ones towards anterior margin, inner surface with large, stout setulae particularly developed towards base; each anterior papilla of aedeagus with lightly pigmented longitudinal strip, distally slender, smooth, tapering to fine point; posterior papilla stout, only gradually tapering to obtuse apex; distiphalus smooth, rather abruptly contracted before acuminate apex; cercus smaller than in *Z. horningi*. Female: sternites 2 to 6 not longer than wide; sternite 4 distinctly divided in two, but others entire or imperfectly divided; tergite 6 not markedly desclerotized on posterior margin; tergite 7 rather similar to that of *Z. minor*, weakly sclerotized rather than desclerotized medially, broad with much of posterior margin transverse (rather than narrowly rounded on each side as in *Z. horningi* and *Z.* sp. 1), with anterior part of tergite extensively shining black and glabrous, with posterior margin (often the only part visible in dried specimens) grey-pruinescent, with anterior apodeme not distinctly forked as it merges with thickened anterior margin of tergite; sternite 7 with pair of sclerites separated by c. twice width of each.

Dimensions. Total length, ♂ 1.3–1.5 mm, ♀ 1.5–1.6 mm; length of thorax, ♂ 0.6–0.7 mm, ♀ 0.6–0.8 mm; length of wing, ♂ 1.5–1.7 mm, ♀ 1.7–1.9 mm.
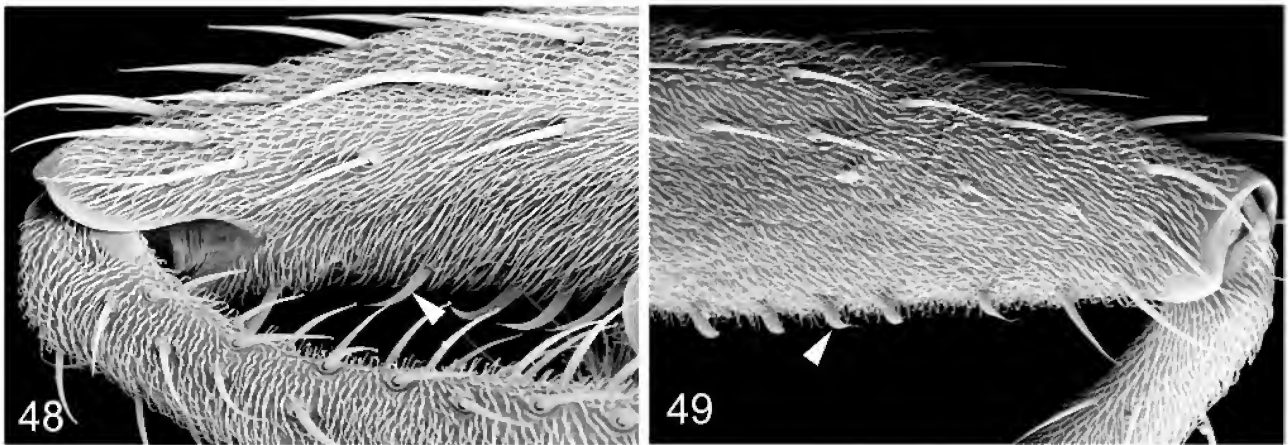
Figs 48, 49. (*48*) *Zalea johnsi*, male, part of right mid femur, posteroventral comb indicated. (*49*) *Z. minor*, the same.

Distribution. New Zealand: South Island—northeast coast and apparently west coast. Only females are available from Jackson's Bay on the west coast. It is desirable that males be obtained from this population to confirm its specific identity.

Notes

Zalea johnsi is very similar to *Z. horningi* which it resembles especially in the well-developed prothoracic precoxal bridge (often not easily visible in dried specimens), the position of the vibrissa very close to anterior extremity of cheek, the relatively long dorsal setulae on the tibiae, and, in the male, the broad, densely microtrichose posterior surstylus. *Zalea johnsi* is most readily distinguished from *Z. horningi* by the characters given in the key, also by those of the aedeagal papillae, distiphallus, and female abdominal sternites, as given in the descriptions. For comparison with other species of the *horningi* group see under those species, and particularly compare the figures of postabdominal structures.

The specific epithet refers to Peter M. Johns in recognition of his generous help and sharing of field knowledge during my field work in New Zealand.
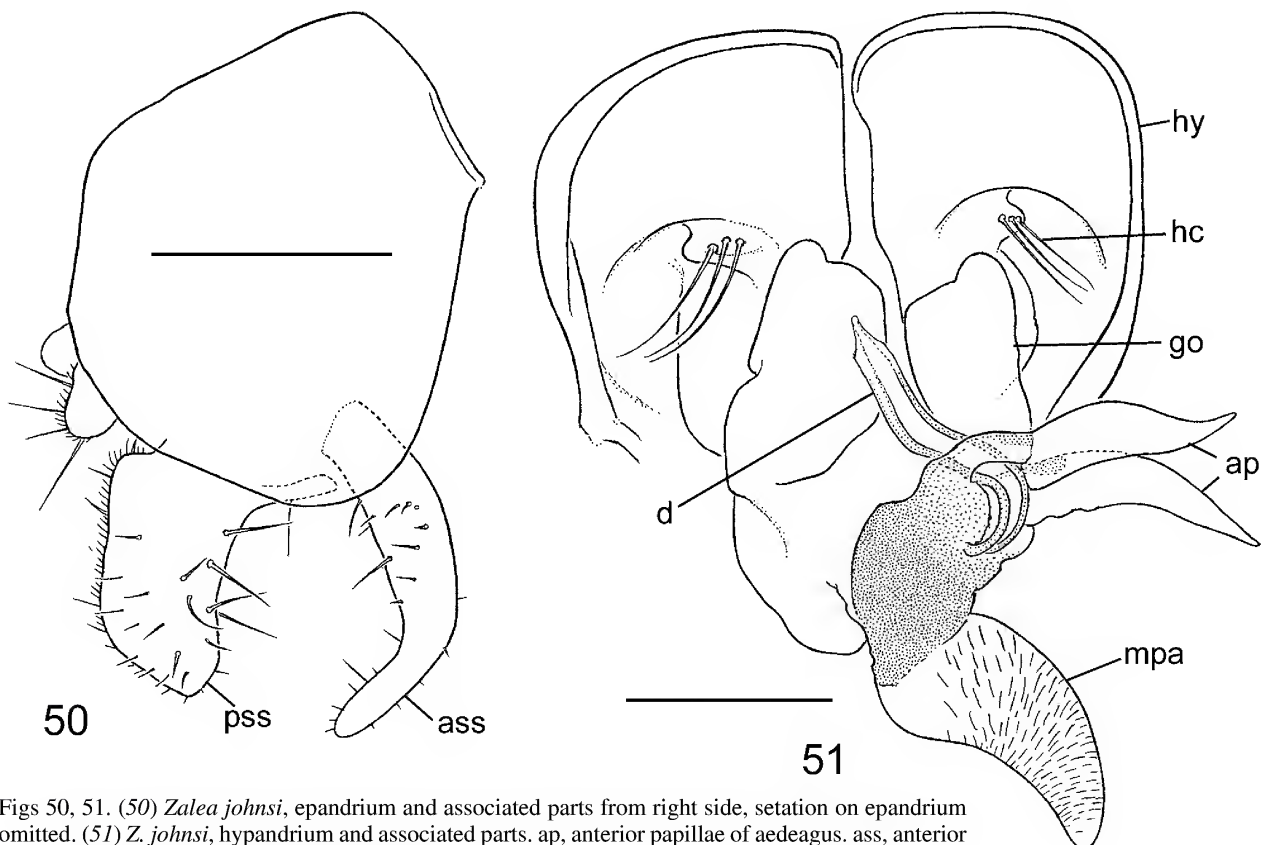
Figs 50, 51. (*50*) *Zalea johnsi*, epandrium and associated parts from right side, setation on epandrium omitted. (*51*) *Z. johnsi*, hypandrium and associated parts. ap, anterior papillae of aedeagus. ass, anterior surstylus. d, distiphallus. go, gonite. hc, hypandrial comb. hy, hypandrium. mpa, median posterior papilla. pss, posterior surstylus. Both scales = 0.1 mm.
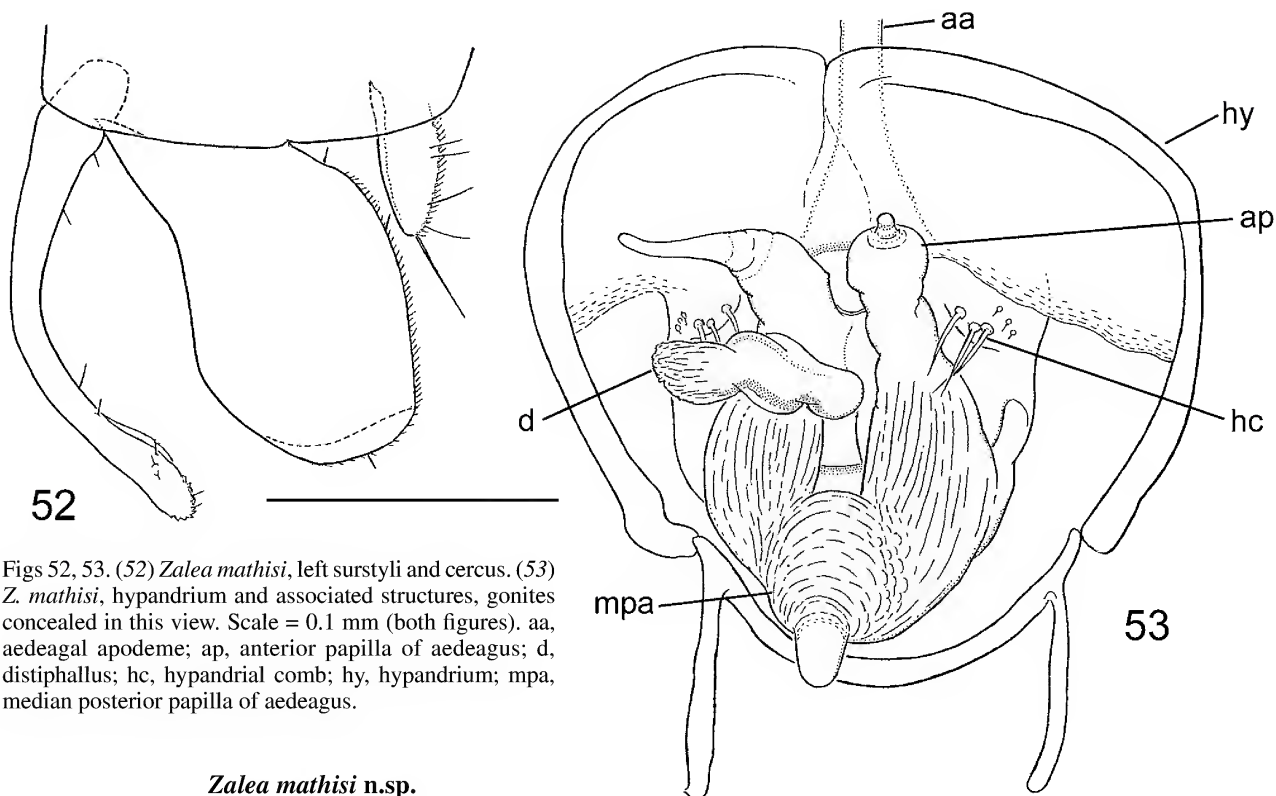
Figs 52, 53. (*52*) *Zalea mathisi*, left surstyli and cercus. (*53*) *Z. mathisi*, hypandrium and associated structures, gonites concealed in this view. Scale = 0.1 mm (both figures). aa, aedeagal apodeme; ap, anterior papilla of aedeagus; d, distiphallus; hc, hypandrial comb; hy, hypandrium; mpa, median posterior papilla of aedeagus.

Zalea mathisi n.sp.

Figs 52, 53

Material examined. HOLOTYPE ♂, New Zealand: Whananaki South (35°31.1'S 174°27.2'E), North Island, 6–8.x.2002, D.M., W.N.M. (NZAC by agreement from USNM, 00184020). Dry-mounted on micro-pin through polyporus pith. PARATYPES New Zealand: 12♂♂, same data as holotype but some 19.ii.1998 (NZAC, AM, USNM); 3♂♂, Sandy Bay (35°33.4'S 174°28.5'E), 6.x.2002, D.M., W.N.M. (USNM).

Description (♂, ♀ unknown). Very similar to *Z. johnsi*, agreeing with description of that species, except as indicated below.

Coloration. Agreeing with that of *Z. johnsi*.

Head. Height of cheek = 0.20–0.28 of height of eye; postvertical bristles generally convergent and proclinate, parallel in one specimen.

Thorax. Wing: cell-4 index = 0.49–0.57.

Abdomen. Anterior surstylus very attenuated but with similar curvature to that of *Z. johnsi*, with scattered, fine setulae, apparently without microtrichia, but densely minutely denticulate on small apical area; posterior surstylus broadly subovate, its distal margin broadly rounded, with no armature on anterior margin, nearly all setulae being scattered on inner surface but not particularly developed towards base, with central to posterior and apical parts of outer surface pruinescent, anterobasal part bare; each anterolateral papilla of aedeagus with slender obtuse apical section; posterior papilla massively swollen and rugose at sides where it overlies basiphallus, tapering to rounded apex; distiphallus rugose distally, not tapered.

Dimensions. Total length 1.2–1.4 mm; length of thorax 0.55–0.67 mm; length of wing 1.3–1.6 mm.

Distribution. New Zealand: North Island, Northland.

Notes

Identification of North Island species in the *horningi* group (other than *Z. earlyi*) relies mainly on male postabdominal characters, especially the shape and armature of the surstyli. Associated females for these are largely absent, but there are indications that the female postabdomen may provide diagnostic characters for at least some species. Males of *Z. mathisi* are distinguished by the very attenuated, weakly setose anterior surstylus and the broadly subovate posterior surstylus with oblique base and very few or no setulae on its outer surface.

The specific epithet refers to Wayne N. Mathis, who collected the type series.

Zalea uda n.sp.

Figs 54, 55

Material examined. HOLOTYPE ♂, New Zealand: Sandy Bay (35°33.4'S 174°28.5'E), 6.x.2002, D.M., W.N.M. (NZAC). Dry-mounted on micro-pin through polyporus pith, genitalia in microvial. PARATYPE 1♂, New Zealand, same data as holotype (USNM).

Description (♂, ♀ unknown). Very similar to *Z. johnsi*, agreeing with description of that species, except as indicated.

Coloration. Agreeing with that of *Z. johnsi*.

Head. Height of cheek = 0.18–0.21 of height of eye; postvertical bristles convergent.

Thorax. Wing: cell-4 index = 0.46–0.48.

Abdomen. Anterior surstylus moderately elongate, compressed, broadest slightly beyond mid-length, very
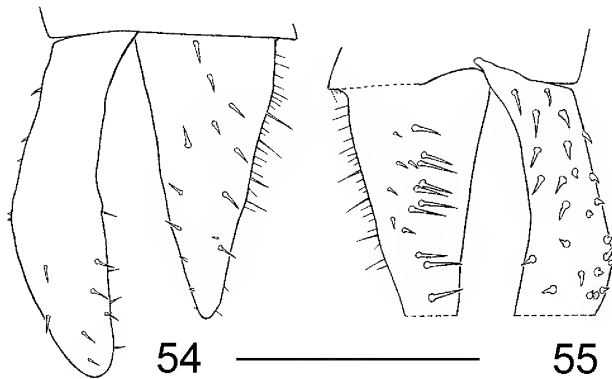
Figs 54, 55. (*54*) *Zalea uda*, left surstyli, outer aspect. (*55*) *Z. uda*, left surstyli, part, inner aspect. Scale = 0.1 mm.

obtuse apically, sparsely setulose on distal half of outer surface, on basal two thirds of inner surface with numerous stout setulae, some of which are short and subconical; posterior surstylus subtriangular, broadest at base, subacute to narrowly obtuse apically, its width at base slightly over half its length, with pruinescence restricted to posterior part of outer surface, with scattered moderately small setulae on outer surface, on inner surface with much larger setulae as well as some small ones, not restricted to basal part; hypandrium and aedeagus with general features of *Z. mathisi*; gonite broad; cercus resembling that of *Z. mathisi*.

Dimensions. Total length c. 1.3 mm; length of thorax 0.57–0.64 mm; length of wing 1.4–1.5 mm.

Distribution. New Zealand: North Island, Northland.

Notes

At present *Z. uda* can only be distinguished from related species of the *horningi* group by the shape and armature of the surstyli. It is conceivable that the female postabdomen may also provide diagnostic characters.

The specific epithet is a Latin adjective meaning wet, in reference to the habitat.

Zalea ohauorae n.sp.

Figs 56, 57

Material examined. HOLOTYPE ♂, New Zealand: Ohauora (or Rocky Point), White Island, North Island vicinity, 6.xii.1966, K.A.W. (AMNZ). "Swept shore landing". Dry-mounted on subtriangular card, genitalia in microvial.

Other material. 1 ♀, same data as holotype (AMNZ).

Description (based on ♂, except where indicated). Very similar to *Z. johnsi*, agreeing with description of that species, except where indicated.

Coloration. Anterior part of postfrons tending to yellowish brown, but not on a defined zone. Palpus tawny.

Head (slightly collapsed in holotype) probably essentially similar to that of *Z. lithax*; vibrissa longer than *Z. lithax* and *Z. johnsi* (see comments below); postvertical bristles probably convergent (displaced in holotype, strongly convergent in associated female).

Thorax. Wing: cell-4 index = 0.55 (0.53 in associated female).

Abdomen. Epandrium with pair of distinct bristles near anterior margin; anterior surstylus slender, rod-like, its apex rounded, slightly expanded, compressed, and curved posteriorly, with some moderately large setulae on inner surface, those near base relatively stout, distal ones slender and quite long, with short microtrichia confined to roughened area at apex; posterior surstylus relatively broad basally with posterior gibbosity, distally slender and scarcely compressed, basal part with irregular group of very large setulae, particularly on posterior part of inner surface, distal part with smaller scattered setulae, with microtrichia concentrated near middle of outer surface; cercus small, with few setulae.

Dimensions. Total length, ♂ c. 1.4 mm (♀ 1.6 mm); length of thorax, ♂ 0.62 mm (♀ 0.68 mm); length of wing, ♂ c. 1.3 mm (♀ c. 1.5 mm); length of vibrissa, ♂ 0.10 mm (♀ 0.11 mm).

Distribution. New Zealand: North Island vicinity. There has been little collecting on White Island, an active volcano, c. 50 km from the shore of North Island in the Bay of Plenty and difficult of access (see Parham, 1973: 19, 119). The habitat of *Z. ohauorae* may have been altered recently by ash clouds (K.A.W. in litt.). There is at present no reason to assume that *Z. ohauorae* is endemic to White Island.

Notes

As with other New Zealand species having convergent postvertical bristles, this species can only be recognized reliably by male genitalia characters. The holotype and one of the two females from the same locality have longer vibrissae than most specimens I assign to *Z. lithax* (measurements given above), but this measurement is not consistent in other species. As indicated above, female abdominal characters are useful for separating *Z. johnsi, Z. lithax* and *Z. horningi*, but good fresh material with abdominal segments extended has
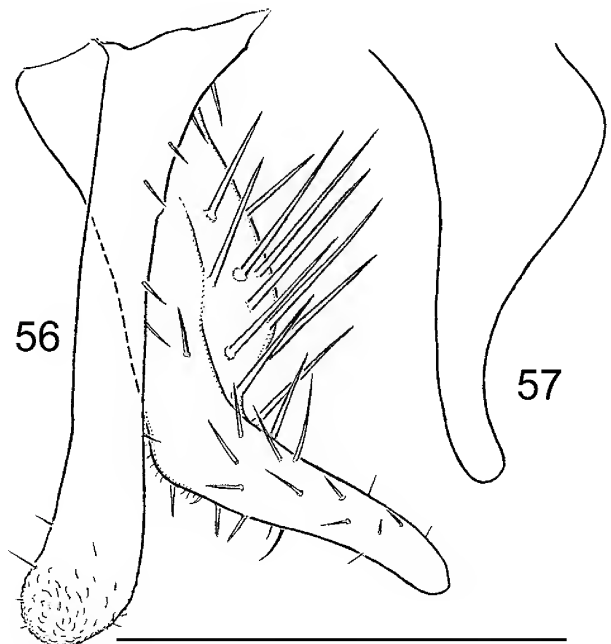
Figs 56, 57. (*56*) *Zalea ohauorae*, right surstyli, anterior view, scale = 0.1 mm. (*57*) the same, left posterior surstylus, approximate outline, outer surface view, not to scale.

not been available for this and some other species.

The specific epithet refers to the type locality and is treated as a Latin noun in the genitive case.

Zalea lithax n.sp.

Figs 58, 59

Material examined. HOLOTYPE ♂, New Zealand: Whanga-parapara Harbour, Great Barrier Island, North Island vicinity, 21.iii.1973, K.A.W. (AMNZ). "Swept stony beach W. side." Dry-mounted on subtriangular card, genitalia in micro-vial. PARATYPES. North Island vicinity: 2♂♂, 1♀, same data as holotype (AM, AMNZ); 3♂♂, 5♀♀, Medlands Beach, Great Barrier Island, 4.xi.2001, J.W.E (AM, AMNZ), in alcohol; 3♂♂, 3♀♀, Awana Bay, Great Barrier Island, 19.ii.2002, J.W.E. (AM, AMNZ), in alcohol; 1♂, Takou Bay (35°6.3'S 173°56.7'E), 7.x.2002, D.M., W.N.M. (NZAC); 5♂♂, Whananaki South (35°31.1'S 174°27.2'E), 6–8.x.2002, D.M., W.N.M. (NZAC, USNM, AM); 1♂, Sandy Bay (35°33.4'S 174°28.5'E), 6.x.2002, D.M., W.N.M. (USNM).

Other material. South Island: 4♂♂, Cable Bay, Nelson district (41°09.6'S 173°24.9'E), 13.ii.1998, W.N.M. (NZAC, USNM, AM).

Description (♂, ♀). Very similar to *Z. johnsi*, agreeing with description of that species, except where indicated.

Coloration. Hypofacial only indistinctly darkened. Palpus dull yellow. Thorax and abdomen as described for *Z. johnsi*. Female: tergite 7 lightly pigmented, with only the narrow apodeme dark.

Head. Height of cheek 0.15–0.22 of height of eye; postvertical bristles rather small, strongly convergent; vibrissa rather short, but not much shorter than anterior peristomial bristles.

Thorax. Wing: cell-4 index = 0.52–0.56.

Abdomen. Male: epandrium with pair of moderately distinct, widely spaced bristles near anterior margin; anterior surstylus slender, rod-like, curved, rounded and compressed at apex, not as long nor as markedly posteriorly directed on distal part as in *Z. johnsi*, with only very fine scattered setulae, except for one or two longer ones on inner surface near base, with microtrichia restricted to inner surface near apex; posterior surstylus extensively microtrichose, more elongate than in *Z. johnsi* and *Z. horningi*, about as long as anterior surstylus (though appearing shorter in Fig. 58), very obtuse at apex, with posterior sub-basal gibbosity, with very few fine setulae anteriorly, and coarser setulae posteriorly, including some on and near posterior gibbosity; cercus short. Female: sternite 1 vestigial; sternites 4 to 6 medially little sclerotized and more or less divided in two; tergite 7 with relatively small anterior apodeme, spreading into broad rami posteriorly, each of which is confluent with a rather broad posterolateral plate; sternite 7 forming pair of plates, each separated from tergite by narrow pleural membrane.

Dimensions. Total length, ♂ 1.3–1.5 mm, ♀ 1.5 mm; length of thorax, ♂ 0.55–0.61 mm, ♀ 0.57–0.68 mm, length of wing, ♂ 1.2–1.5 mm, ♀ 1.5–1.6 mm.

Distribution. New Zealand: North Island vicinity—Great Barrier Island and Northland. South Island—far north.
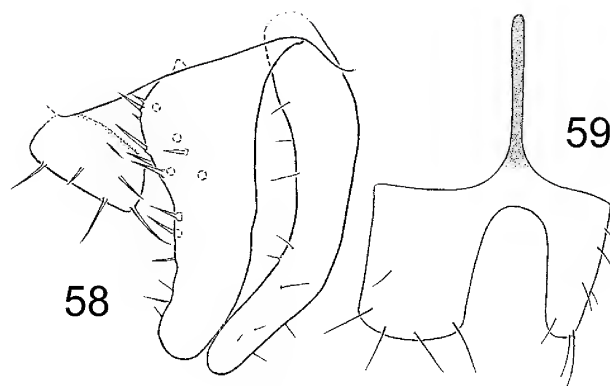
Figs 58, 59. (*58*) *Zalea lithax*, right surstyli and cercus, slightly posterior of lateral view, posterior surstylus slightly foreshortened apically through curvature, scale = 0.1 mm. (*59*) *Zalea lithax*, tergite 7 of female, precise dorsal view, but left lateral plate spread flat, right plate shown in round.

Notes

Recognition of this species depends largely on postabdominal characters in both sexes, but there is no evidence of such closely related species as *Z. mathisi* and *Z. ohauorae* inhabiting Great Barrier Island or the vicinity.

The specific epithet is a Greek adjective meaning stony, in reference to the habitat.

Zalea earlyi n.sp.

Figs 60, 61

Material examined. HOLOTYPE ♀, New Zealand: Medlands Beach, Great Barrier Island, North Island vicinity, 4.xi.2001, J.W.E. (AMNZ). "Intertidal rocks ... swept L11022." In alcohol. PARATYPE. 1♀, New Zealand: Ike Island, Noisies Islands, Hauraki Gulf, North Island vicinity, 9.xii.1979, K.A.W. (AMNZ). Dry-mounted on card.

Description (♀, ♂ unknown). Somewhat similar to *Z. johnsi*, agreeing with description of that species, except as indicated.

Coloration (based mainly on dry-mounted paratype). Postfrons rusty-brown, with orbits and frontal triangle dark greyish; face, parafacial and cheek pale yellowish; hypofacial and prelabrum pale grey. Palpus tawny-yellow. Halter dull yellowish. Abdomen: anterior section of tergite 7 quite black, its lateral plates grey-brown; cercus grey-brown.

Head and eye both higher than long; height of cheek c. 0.30 of height of eye; face slightly concave; vibrissal angle not prominent in profile; postgenal setulae well developed, c. four of them forming an almost vertical series; postvertical bristles slightly divergent to almost parallel, a little smaller than ocellars and larger fronto-orbitals. Palpus slightly clavate.

Thorax. Prosternum with narrow, distinct precoxal bridge. Mid femur without differentiated posteroventral bristles; fore tibia with several dorsal setulae almost as long as tibial diameter; those on mid and hind tibiae shorter. Wing: cell-4 index = 0.54–0.59.

Abdomen. Sternite 1 divided into two well developed but widely separated plates; sternites 3 to 6 well sclerotized, undivided; tergite 6 not noticeably sinuate or desclerotized
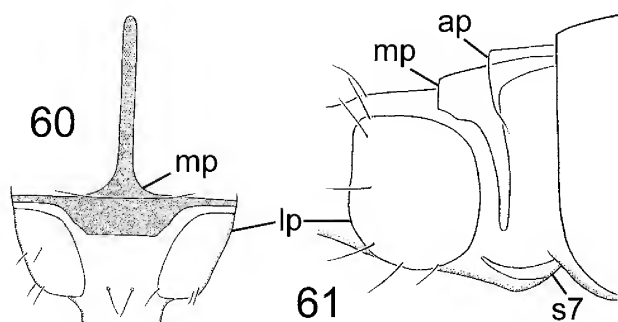
Figs 60, 61. (*60*) *Zalea earlyi*, female, dorsal view of abdominal segment 7, showing tripartite tergite. (*61*) the same, right lateral view of segment 7. *ap*, pouch containing apodeme; *lp*, lateral plate of tergite 7; *mp*, anteromedian plate of tergite 7 with apodeme; *s7*, sternite 7.

on posterior margin; tergite 7 with separate anteromedian and paired posterolateral plates; anteromedian plate smooth with long anterior apodeme and pair of slender lateral arms arising from short central plate; each lateral plate rather short, about as broad as long, setulose; dorsal membrane between lateral plates with pair of setulae; sternite 7 apparently divided into two plates but details not observed.

Dimensions. Total length 1.8 (dried, abdomen deflexed)-2.3 mm; length of thorax 0.93–0.98 mm; length of wing 2.0 mm.

Distribution. New Zealand: North Island vicinity—Great Barrier Island and Hauraki Gulf.

Notes

Zalea earlyi resembles other New Zealand *Zalea* species with prothoracic precoxal bridge (e.g., *Z. horningi*, *Z. johnsi* etc.), but these all lack the well-developed set of postgenal setulae, and the females, where known, do not have tergite 7

divided into three separate plates. *Zalea wisei* and sp. 1 have similar postgenal setulae, but lack the precoxal bridge and have apical scutellar setulae and much smaller C-4 index; the latter species has female sternite 7 in one piece, though deeply lobed.

Although the male is unknown and female material is minimal, there is adequate evidence that the species is distinct, and the unusual postabdominal characters should ensure reidentification of females.

The specific epithet refers to John W. Early who collected the holotype and other useful material of *Zalea* for this project.

Zalea horningi (Harrison)

Figs 20, 62–65

Tethina horningi Harrison, 1976: 143, fig. 3.
*Zalea horningi* (Harrison).–D. McAlpine, 1985: 82.

Material examined. HOLOTYPE ♂, New Zealand: Seal Cove, Snares Islands, 2.1.1972, D.S.H. (NZAC). Dry-mounted on card-point, postabdomen now placed in microvial attached to pin. PARATYPES. As listed by Harrison. I examined 2♂♂, 2♀♀ from NZAC in 1982 but details of the postabdomens were not then studied.

Other material (localities only). South Island: Kaikoura Peninsula (AM); Sumner, near Christchurch (AM, BM); Laverick's Bay, near Akaroa (AM, NZAC); Otanerito Bay, near Akaroa (AM, NZAC); Pilot Beach, Otago Peninsula (USNM).

Supplementary description

Very similar to *Z. johnsi* and agreeing with description of that species except as indicated below.

Coloration. Abdomen of female: paired sclerites of tergite 7 dull yellowish, black anteriorly, dull grey on small posterior zone.
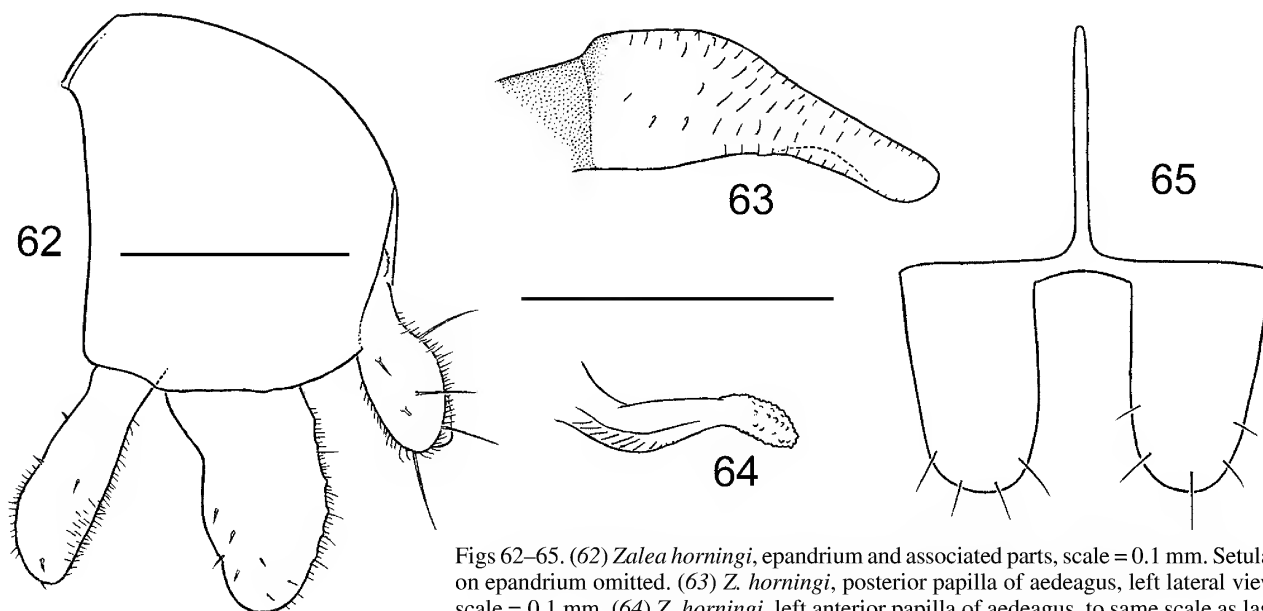
Figs 62–65. (*62*) *Zalea horningi*, epandrium and associated parts, scale = 0.1 mm. Setulae on epandrium omitted. (*63*) *Z. horningi*, posterior papilla of aedeagus, left lateral view, scale = 0.1 mm. (*64*) *Z. horningi*, left anterior papilla of aedeagus, to same scale as last. (*65*) *Zalea horningi*, tergite 7 of female, part of lateral outline approximate only.

Head. Postvertical bristles small, convergent.

Thorax. Wing: cell-4 index = 0.50 (holotype), 0.53–0.59 (South Island material).

Abdomen. Male: anterior surstylus, almost straight but slightly incurved, rounded and compressed apically, with short setulae mainly on inner surface, with no particularly developed setulae on posterior surface, extensively microtrichose, mainly on inner surface of distal half; posterior surstylus broadly rounded apically, with at most only slight posterior basal incision, microtrichose on large part of inner and outer surfaces, with few small setulae on outer surface, with larger setulae in inner surface, of which a few more basal ones are particularly large; each anterior aedeagal papilla not smooth and evenly tapering as in *Z. johnsi*, but with zone of transverse ridges near mid-length, and slender, obtuse, roughly pustulose apical part; posterior papilla with many short, transverse surface ridges, slightly narrowed well before apex to form somewhat transversely compressed distal part with anterior concavity and rather thick rounded apex; distiphallus a little broader distally than in *Z. johnsi*, with less finely pointed, slightly irregularly incised apical part. Female: sternites generally as in *Z. johnsi*; sternites 2 to 6 all divided in two or almost so; tergite 7 (Fig. 65) very deeply divided, somewhat like that of *Z. dayi* but with more elongate anterior apodeme.

Distribution. New Zealand: South Island; Snares Islands.

Notes

The key to species and the above comparative description gives all the points of difference from *Z. johnsi* that I am able to confirm. The convergent postvertical bristles of this species provide a remarkably consistent difference from *Z. johnsi*, and associate *Z. horningi* with the four species *Z. lithax, Z. mathisi, Z. uda*, and *Z. ohauorae*, which are recorded at present only from North Island vicinity.

The above description of postabdominal characters is based mainly on South Island specimens. I have examined the epandrium and surstyli of the holotype which resemble those of South Island material. As further dissection of this specimen may have proved destructive, details of the hypandrium and aedeagus have not been checked for the Snares Island population.
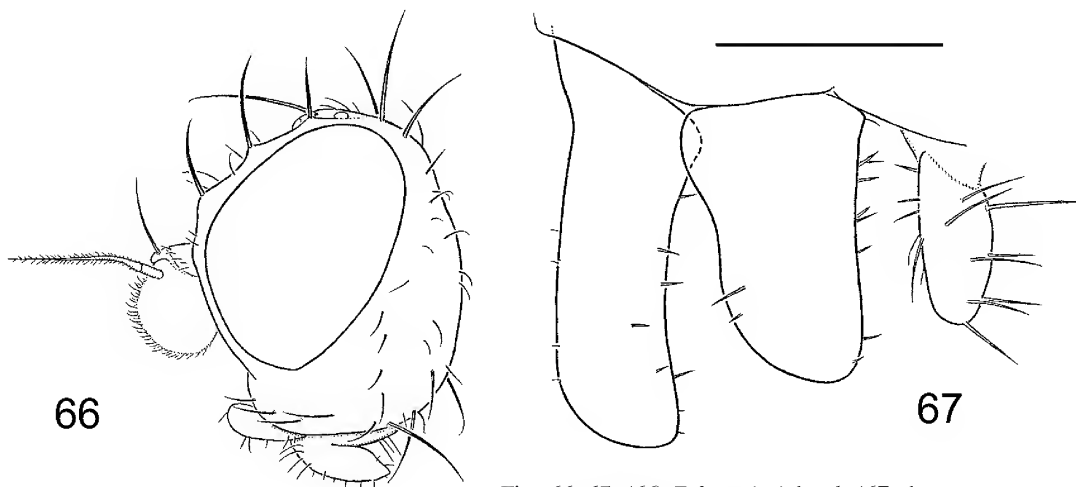
Zalea wisei n.sp.

Figs 66, 67, 71

Material examined. HOLOTYPE ♂, New Zealand: Otata Island, Noisies Islands, Hauraki Gulf, North Island vicinity, 8.xii.1979, K.A.W. (AMNZ). "Swept at low tide. Intertidal rocks, N. coast." Mounted on card point impaled directly on pin. PARATYPE. 1 ♂, identical data to holotype (AMNZ). Mounted on card point glued to square card on pin.

Description (♂, ♀ unknown). Size larger than that of most New Zealand *Zalea* spp.; habitus rather stout.

Coloration. Head dark grey to greyish brown; postfrons without yellowish or other pale zones; parafacial, face, and cheek grey-pruinescent. Antenna greyish-tawny. Prelabrum grey or partly blackish; palpus tawny yellow. Thorax dark grey-pruinescent, brown-pruinescent dorsally. Legs dark grey-brown; tarsi more tawny-brown, mostly darker apically. Wing membrane tinged with smoky-grey; veins brown. Halter yellow. Abdomen dark grey-brown.

Head higher than long; eye, in profile, obliquely oval, 1.25–1.27 times as high as long; triangle formed by joining centers of ocelli not broader than equilateral triangle; postfrons narrowed anteriorly so that minimum separation of eyes = 0.36 of total width of head; face concave; vibrissal region not very prominent; cheek 0.25–0.26 of height of eye; postvertical bristles strongly divergent; ocellar bristles very slightly closer together than are posterior ocelli; posterior fronto-orbital bristle not at all reclinate, curved outwards; vibrissa smaller than anterior peristomial bristles; postgenal region with vertical series of four or five setulae. Antenna: segment 5 3.6 times as long as wide; palpus extending beyond prelabrum when proboscis withdrawn.

Thorax. Prosternum without bridge, widely separated from propleuron on each side; proepisternal bristle well developed (compared with *horningi* group); mesopleuron with two large bristles near posterior margin; scutellum with pair of setulae between bristles of apical pair, each c. half as long as apical bristle. Fore tibia usually with three posterodorsal bristles longer than tibial diameter; mid and hind tibiae with several long dorsal setulae or bristles. Wing: cell-4 index = 0.39–0.43.

Figs 66, 67. (*66*) *Zalea wisei*, head. (*67*) the same, left surstyli and cercus, scale = 0.05 mm.

Abdomen. Epandrium broad, rounded, with two pairs of large dorsal bristles and smaller setulae; surstyli (Fig. 67) with short setulae and no apparent microtrichia; hypandrium and associated structures not elucidated.

Dimensions. Total length 2.2–2.3 mm; length of thorax 1.1 mm; length of wing 2.2–2.4 mm; width of epandrium (dried) 0.34 mm.

Distribution. Only known from the Noisies (or Noises) Islands in Hauraki Gulf, North Island vicinity, New Zealand. These are a group of islets and rocks near Auckland. "Otata Island" is 38°42'S 174°58'E in Gazetteer.

Notes

Zalea wisei and the closely related "sp. 1" differ from other New Zealand *Zalea* spp. in the non-reclinate posterior fronto-orbital bristle, absence of the prothoracic precoxal bridge, longer proepisternal bristle, presence of a pair of setulae between the apical scutellar bristles, presence of two large posterior mesopleural bristles, and smaller C-4 index. For comparison with sp. 1 see under that species.

The specific epithet refers to Keith A.J. Wise, who collected the type material and other significant material of *Zalea*.

Zalea sp. 1

Figs 21, 68–70

Material examined. 1 ♀, New Zealand: Otanerito Bay [north side of beach, on shoreline rocks], near Akaroa, South Island, 1.ii.2001, B.J.D., D.K.M. (AM). Otanerito Bay is also known as Long Bay, but there is another Long Bay, also on Banks Peninsula.

Description (♀, male unknown). The only known specimen resembles *Z. wisei* in many characters but is larger and more elongate.

Coloration. Head grey-black to brown-black. Antenna dark grey to brown black. Prelabrum blackish, with grey pruinescence; palpus brownish, with grey pruinescence. Halter tawny, with creamy capitellum. Abdomen brown-black; paired sclerites of tergite 7 shining black, grey-brown-pruinescent on short posterior section.

Head much higher than long; eye, in profile, subcircular, but for slight ventral extension, 1.1 times as high as long; triangle formed by joining centres of ocelli broader than equilateral triangle; cheek most prominent posteroventrally, height of cheek 0.25 of height of eye; postvertical bristles rather long, c. as long as anterior fronto-orbital, perhaps nearly parallel (one slightly displaced); ocellar bristles more closely placed than in other species. Palpus moderately short and thick, not extending anteriorly beyond prelabrum when proboscis withdrawn.

Thorax. Prosternum without precoxal bridge; anterior dorsocentral and proepisternal bristles longer than in other species. Wing: cell-4 index = 0.35.

Abdomen. Sternites 1 to 5 all broad and well sclerotized, undivided; tergite 7 rather like that of *Z. dayi*, medially divided to c. as far forward as fork of anterior apodeme (which is not exposed to view), each of paired sclerites somewhat elongate, rounded posteriorly, with several long setulae.

Dimensions. Total length (abdomen extended) 3.0 mm; length of thorax 1.2 mm; length of wing 2.9 mm.

Distribution. New Zealand: only known from Banks Peninsula, South Island.

Notes

Because of the similarity between this species and *Z. wisei* and the paucity of material, which prevents comparison between the same sex of each species, I refrain from naming this species at present. The extent of the differences between the samples seems to indicate specific distinction, but I have had to use subjective judgement in providing key characters. The single specimen of species 1 differs in having the eye in profile 1.12 times as high as long (1.25–1.27 in *Z. wisei*), triangle formed by joining centres of ocelli broader than equilateral triangle (not broader than such in *Z. wisei*), postfrons not much narrowed anteriorly, so that minimum separation of eyes = 0.40 of width of head (postfrons more narrowed anteriorly, so that minimum separation of eyes =
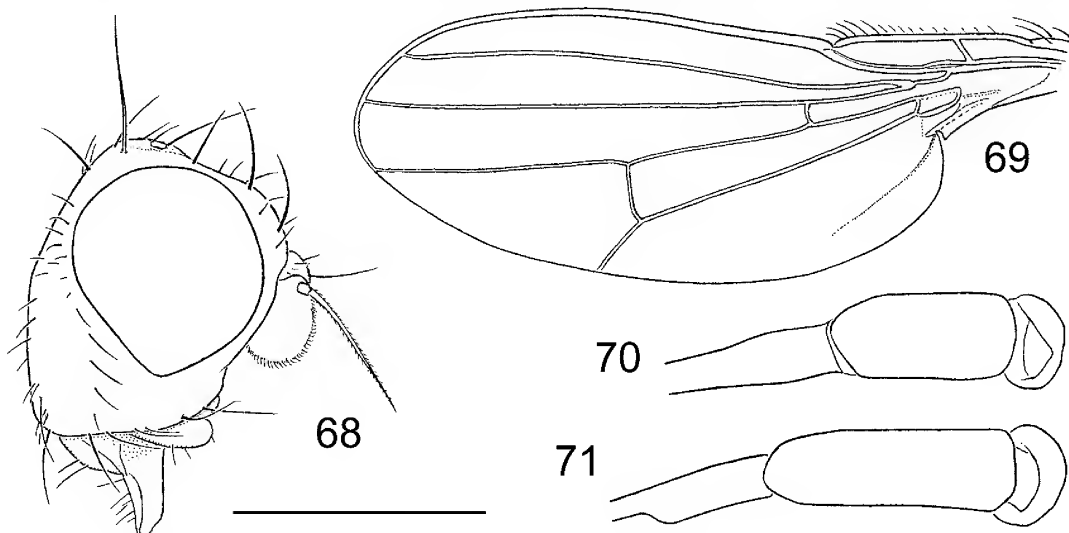
Figs 68–71. (*68–70*) *Zalea* sp. 1, (*68*) head; (*69*) wing; (*70*) base of arista. (*71*) *Z. wisei*, base of arista, scale (for Figs 70, 71 only) = 0.05 mm.

0.36 of width of head in *Z. wisei*), cheek region, in outline, descending and most prominent posteriorly (cheek region not more ventrally prominent posteriorly than anteriorly in *Z. wisei*), postvertical bristles at most slightly divergent (strongly divergent in *Z. wisei*), ocellar bristles markedly closer together than are posterior ocelli (very slightly closer together than are posterior ocelli in *Z. wisei*), antennal segment 3 blackish, brown on small part of ventral margin only (antennal segment 3 brown to tawny-brown above, tawny-yellow below in *Z. wisei*), antennal segment 5 2.2 times as long as wide (3.6 times as long as wide in *Z. wisei*), palpus brownish, not projecting anteriorly beyond prelabrum when proboscis withdrawn (palpus deep yellow, projecting distinctly beyond prelabrum in *Z. wisei*), cell-4 index = 0.35 (0.39–0.43 in *Z. wisei*).

Zalea sp. 2

Material examined. 1♀, New Zealand: Beach, N end Mitimiti, N of Hokianga Harbour, North Island, 4.ii.1988, R.F. Gilbert (AMNZ).

Description. The single specimen in moderate condition is inadequate for a formal description.

Notes

This specimen is distinct from any other available New Zealand specimens and tends to run near *Z. minor*, which it superficially resembles, in the key. Prothoracic precoxal bridges appear to be absent, and the postvertical bristles are divergent. However, in the presence of two longer posterodorsal bristles on the fore femur and less prominent vibrissal angle it more closely resembles such New Zealand species as *Z. johnsi*. The separation of the two lateral plates of tergite 7 from each other seems to be more complete than in *Z. minor*. Without better material, it has not been possible to place it satisfactorily in the key to species.
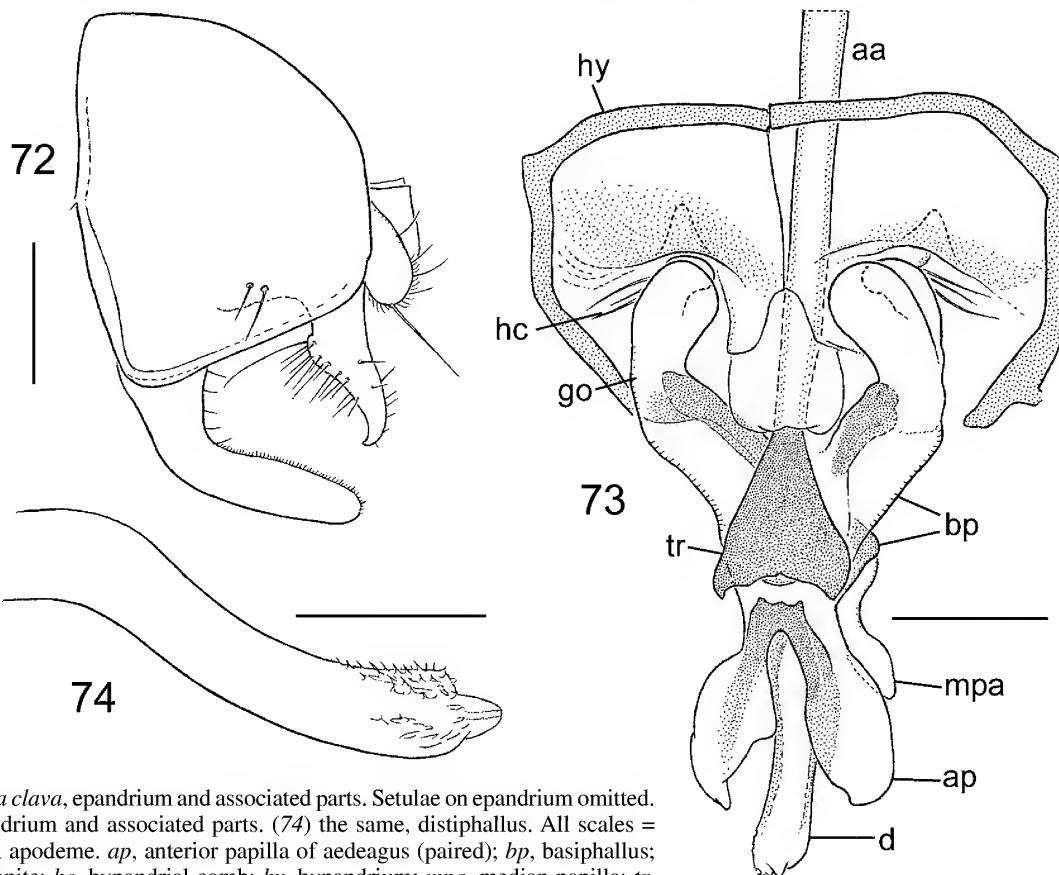
Zalea clava n.sp.

Figs 72–75

Material examined. HOLOTYPE ♀, Western Australia: Cable Beach (foot of cliffs W of beach), S of Albany (35°07'02"S 117°53'51"E), 29–30.xi.1998, B.J.D., D.K.M. (WAM). PARATYPES. Western Australia: 4♂♂, 3♀♀, same data as holotype (AM, USNM); 1♂, 2♀♀, Canal Rocks, near Yallingup, 33°39'42"S 115°00'35"E, 23.xi.1998, B.J.D., D.K.M. (AM); 1♂, Ellensbrook Beach, near Margaret River, 33°54'17"S 114°59'16"E, B.J.D., D.K.M. (AM).

Description (♂, ♀). General characters as given for subfamily and for genus *Zalea*.

Coloration generally as given for *Z. dayi*. Thoracic pleura greyer than in *Z. dayi*; mesopleuron with little or no brown suffusion. Legs, especially femora, greyer than in *Z. dayi*; tarsi brown to tawny-brown. ♂: anterior surstylus tawny, more shining on outer surface than in *Z. minor* and *Z. dayi*, through more restricted pruinescence. ♀: paired sclerites of sternite 7 predominantly black, grey-pruinescent only at posterior extremities; tergite 7 pruinescent, brownish grey; sternite 7 largely shining black; cercus brownish, usually darker both apically and near base.

Figs 72–74. (72) *Zalea clava*, epandrium and associated parts. Setulae on epandrium omitted. (73) the same, hypandrium and associated parts. (74) the same, distiphallus. All scales = 0.1 mm. *aa*, aedeagal apodeme. *ap*, anterior papilla of aedeagus (paired); *bp*, basiphallus; *d*, distiphallus; *go*, gonite; *hc*, hypandrial comb; *hy*, hypandrium; *mpa*, median papilla; *tr*, triangular sclerite of basiphallus.
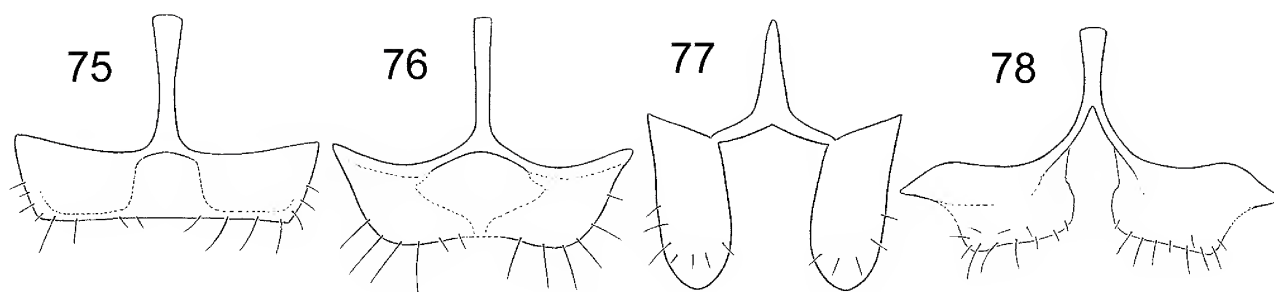
Figs 75–78. Tergite 7 of *Zalea* females, semi-diagrammatic. *(75)* Z. *clava*. *(76)* Z. *minor*. *(77)* Z. *dayi*. *(78)* Z. *major*.

Head. Height of cheek c. 0.26–0.32 of height of eye; postvertical bristles subparallel to slightly divergent. Antenna similar to that of Z. *minor* and Z. *dayi* in proportions. Palpus clavate, much more thickened distally than in other *Zalea* spp., and usually distinctly more than half as deep as cheek or antennal segment 3 (though depth of both these rather variable).

Thorax. Chaetotaxy and most leg characters as for genus. Mid femur of male with loose distal comb of variably short, thick posteroventral bristles, either all quite blunt or some pointed; mid femur of female without differentiated posteroventral bristles. Fore tibia with one long dorsal bristle slightly beyond mid-length; mid tibia with one long dorsal bristle near mid-length; hind tibia often with few irregular long setulae or fine bristles. Vein 2 usually more strongly arched than in Z. *minor*; cell-4 index = 0.58–0.65.

Abdomen. Male: anterior surstylus very elongate, pruinescent, but extensively smooth and shining on outer surface; posterior surstylus not pruinescent, narrowly obtuse at apex, with long-setulose anterior gibbosity beyond base; hypandrium and aedeagus resembling those of Z. *minor*; posterior papilla of aedeagus smaller; distiphallus with denticles finer and less dense, and without distinctly pigmented longitudinal strips. Female: sternites 3 to 6 broader than in Z. *minor* and Z. *major*, but much less so than in Z. *dayi*, all undivided; tergite 7 undivided, somewhat sclerotized and pigmented across whole width, but weakly sclerotized centrally and on posterior margin, with broad, strongly sclerotized plate on each side, and with lateral arms of anterior apodeme short; paired sclerites of sternite 7 much broader than in Z. *minor* and Z. *major*, quite narrowly separated medially.

Dimensions. Total length, ♂ 1.8–1.9 mm, ♀ 2.1–2.4 mm; length of thorax, ♂ 0.77–0.90 mm, ♀ 0.86–0.96 mm; length of wing, ♂ 1.8–2.0 mm, ♀ 2.0–2.2 mm.

Distribution. Western Australia: southern coast, S of 33°30'S.

Notes

Zalea clava is distinguishable from all other *Zalea* spp. by its very strongly clavate palpus. It is the only known Australian species with a long dorsal bristle on the fore and mid tibia, and, unlike the New Zealand, species this is an isolated bristle near or slightly beyond mid-length.

The specific epithet is a Latin noun referring to the clavate palpus.

Zalea minor (D. McAlpine)

Figs 16, 26, 33, 49, 76

Zale minor D. McAlpine, 1982: 110–112, figs 4–9.
Zalea minor (D. McAlpine).–D. McAlpine, 1985: 82.

Material examined. HOLOTYPE ♂, New South Wales: Bottle and Glass Rocks, Vaucluse, near Sydney [Nielsen Park, Sydney Harbour], 25.i.1964, D.K.M. (AM).

Other material (localities only). New South Wales: Wategos Beach, Cape Byron (AM); Broken Head, near Byron Bay (AM, ANIC, MV); Woolgoolga (AM); Smoky Cape, near South West Rocks (AM); Black Head (Haliday's Point), Taree district (AM); The Ruins, Booti Booti National Park, Forster district (AM); Seal Rocks (headland) (AM, NZAC, BPB, MCV, ZMC); Forrester's Beach, near Terrigal (AM); Grotto Point, Sydney Harbour (AM); Currarong (AM); Broulee Beach (ANIC). Victoria: Walkerville (AM); Bunnarong Cliffs, near Inverloch (AM). Tasmania: Binalong Bay, near Saint Helen's (AM, TDA); Spring Beach, near Orford (AM); Stapleton Beach, near Orford (AM); Tesselated Pavement, Eaglehawk Neck (AM); Gilham's Beach, Research Bay (AM, ANIC, TDA). See also paratype list of D. McAlpine (1982, material from Sydney district).

Supplementary description

Thorax. Mid femur of male with inconspicuous posteroventral comb of few short, thick, very blunt bristles beyond mid-length, and generally with a separate series of few fine, longer posteroventral bristles mostly before mid-length; that of female without differentiated posteroventral bristles.

Abdomen. Sternite 1 undivided; sternite 2 with deep anterior incision somewhat as in Z. *major*. Male: hypandrium on each side with compact comb of three long bristles and group of three minute slender setulae, not shown in my previous figure (D. McAlpine, 1982: fig. 8) because of partial concealment by gonites. Female: sternites 2 to 5 narrow; sternite 6 completely or incompletely divided into two sclerites which diverge posteriorly; tergite 7 (Fig. 76) with lightly sclerotized or almost desclerotized central zone extending only narrowly to posterior margin, which is broadly transverse; paired sclerites of sternite 7 elongate-oval, broadened and more approximated on anterior margins.

Dimensions. In the original description, for "width of hypandrium", read "width of epandrium".
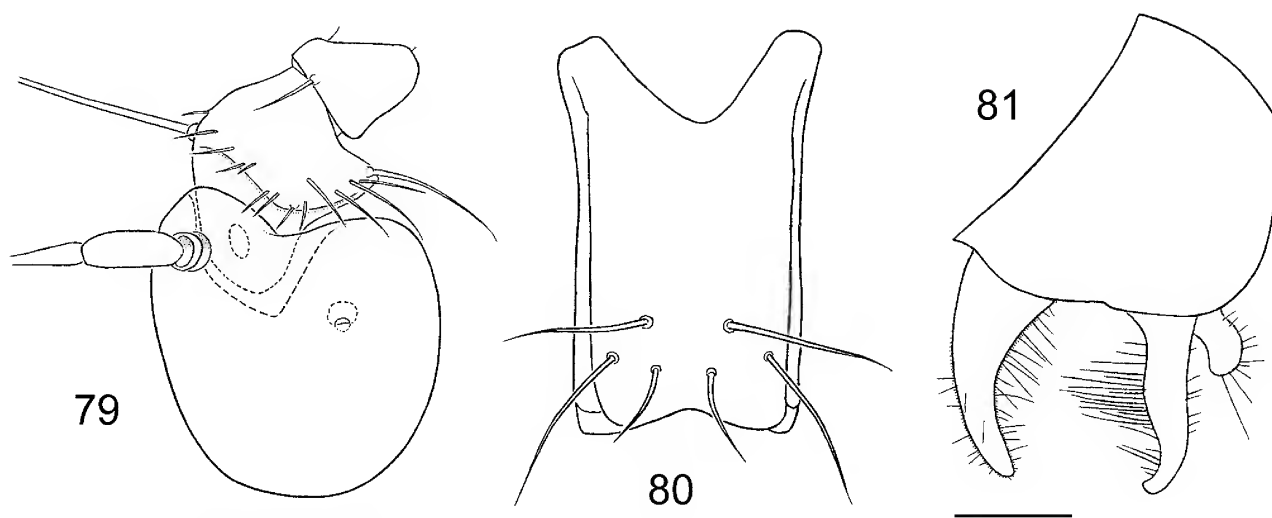
Figs 79–81. *Zalea major*. (*79*) left antenna, scale = 0.1 mm. (*80*) prementum of proboscis. (*81*) epandrium and associated parts, left lateral view, scale = 0.1 mm. Setulae on epandrium omitted.

Distribution. New South Wales: coasts generally. Victoria: coasts east of Port Phillip. Tasmania: widely distributed on east coast, and probably other coastal districts which have not yet been searched for intertidal flies.

Notes

Zalea minor is the most abundant species of *Zalea* in New South Wales and Tasmanian habitats. It is distinguished as indicated in the above key.

Zalea major (D. McAlpine)

Figs 22, 43, 78–84

Zale major D. McAlpine, 1982: 112, figs 1–3.
*Zalea major* (D. McAlpine).–D. McAlpine, 1985: 82.

Material examined. HOLOTYPE ♀, New South Wales: Bundeena, Port Hacking, 10.xii.1966, D.K.M. (AM). The statement (D. McAlpine, 1982) that the holotype is a male is a typographical error.

Other material (localities only). New South Wales: Wategos Beach, Cape Byron (AM); Broken Head, near Byron Bay (AM, ANIC); Smoky Cape, near South West Rocks (AM); The Ruins, Booti Booti National Park, Forster district (AM, BPB, MCV, USNM); Seal Rocks (headland) (AM, ANIC); Forrester's Beach, near Terrigal (AM); Grotto Point, Sydney Harbour (AM); Kurnell, Botany Bay. Tasmania: Binalong Bay, near Saint Helen's (AM, TDA); Ironhouse Point, near Falmouth (AM). See also paratype list of D. McAlpine (1982, material from Gosford and Sydney districts).

Supplementary description

Antenna. Segment 3 and palpus plain yellow in male, usually slightly suffused with brown in female.

Legs. Mid femur of male with strong distal posteroventral comb of short, thick, blunt bristles, with fewer longer posteroventral bristles near and before middle; mid femur of female with no differentiated posteroventral bristles; tibiae without differentiated long bristles.
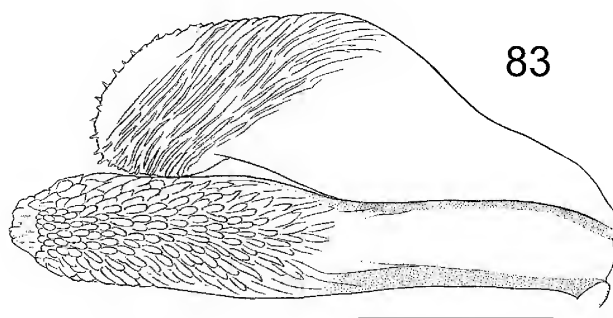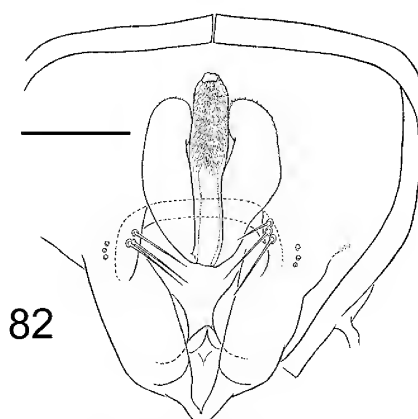
Figs 82, 83. *Zalea major*. (*82*) hypandrium and associated parts, scale = 0.1 mm. (*83*) distiphallus and left anterior papilla of aedeagus, scale = 0.05 mm.

Abdomen. Male: epandrial structures resembling those of *Z. minor* including extensively pubescent anterior surstylus and non-pruinescent posterior surstylus; anterior surstylus expanded at base, gradually narrowed distally; posterior surstylus relatively thick on basal half, tapering beyond, subtruncate at apex, with group of long dense setulae anteriorly near mid-length; ventral plate of epandrium with two well separated setulae on each side; hypandrium on each side with group of three large bristles, of which sockets are contiguous, and three small stumpy setulae laterad of
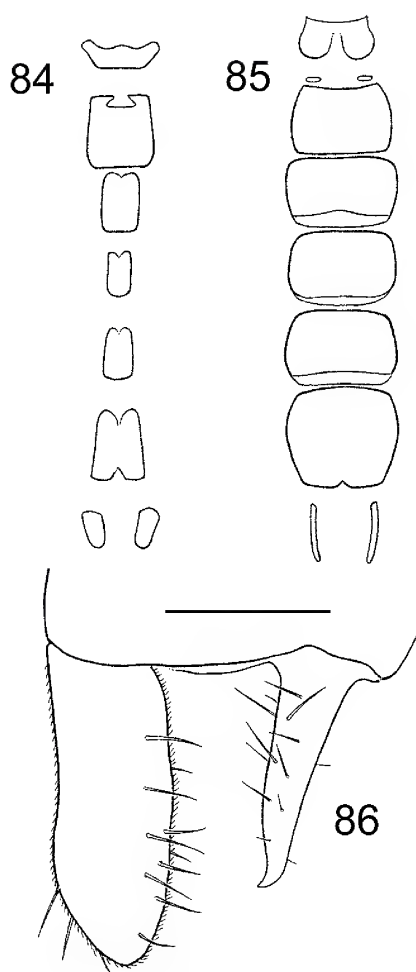
Figs 84–86. (*84*) *Zalea major*, abdominal sternites 1–7 of female, semi-diagrammatic. (*85*) *Zalea dayi*, the same. (*86*) *Z. dayi*, left surstyli, scale = 0.1 mm.

these; each anterior papilla of aedeagus with numerous parallel ridges, pustulose distally, apically with pustules becoming slender and thorn-like; median posterior papilla very small; distiphallus on posterior surface pustulose from near mid-length almost to apex, pustules becoming crowded distally, mostly rounded, some lateral ones obtusely pointed, forming extensive file-like surface. Female: sternite 1 not deeply divided; sternites 3 to 5 narrow, longer than broad; sternite 6 medially notched on both anterior and posterior margins; tergite 6 desclerotized on posterior margin medially, broader than tergite 5, with posteroventral part more strongly produced; tergite 7 (Fig. 78) divided in two, each sclerite broader than long, grey pruinescent, black only where it joins lateral arm of anterior apodeme; paired sclerites of sternite 7 not very narrow, separated from each other by less than 3× width of each, each with c. three posterior setulae; cercus slightly shorter than in *Z. minor* and *Z. dayi*.

Dimensions. In the original description, for "width of hypandrium", read "width of epandrium".

Distribution. Coastal New South Wales, from Byron Bay district to Port Hacking (Bundeena). Tasmania: east coast, north from Falmouth district.

Notes

Most specimens of *Z. major* can be distinguished from the sympatric *Z. minor* and *Z. dayi* by their larger size. Males can further be distinguished by the much broader epandrium and differently shaped surstyli, and females can be distinguished by the differently shaped tergites 6 and 7.

Zalea dayi n.sp.

Figs 13, 38, 77, 85, 86

Material examined. HOLOTYPE ♀, New South Wales: Seal Rocks (headland, north side), 11.x.2000, D.K.M. (AM). Dry-mounted on triangular point. PARATYPES. New South Wales: 4♂♂, 4♀♀, Black Head (Haliday's Point), Taree district, 13.ix.2000, B.J.D. (AM, USNM); 11♂♂, 7♀♀, "The Ruins", Booti Booti National Park, Forster district, 15.ix.2000, B.J.D. (AM, ANIC); 35♂♂, 30♀♀, Seal Rocks, 26.ix.2000, 9–11.x.2000, D.J.B., D.K.M. (AM, ANIC, BM, BPB, CNC, TAU, USNM). Material from Black Head and "The Ruins" in alcohol; that from Seal Rocks mostly dry-mounted on points or micro-pins with abdomens extended.

Other material. New South Wales: 1♀, Vaucluse, Sydney Harbour, 25.i.1964, D.K.M. [AM, originally determined as a paratype of *Z. minor* (D. McAlpine)].

Description (♂, ♀). Very small dull, dark greyish fly, with unmarked wing, with general characters as for genus *Zalea*.

Coloration. Head predominantly brown, with brown to grey pruinescence; anterior part of postfrons yellowish brown; parafacial and upper part of cheek pale yellow to greyish yellow. Antenna yellow; segment 3 often with slight tawny suffusion; arista dark brown. Prelabrum grey; palpus yellow. Thorax with brown-black ground colour, densely covered with grey to brown pruinescence; bristles black. Legs dark grey-brown. Wing membrane uniformly smoky grey; veins brownish. Halter yellow basally, with creamy capitellum. Abdomen dark grey-brown, almost entirely pruinescent; in male, anterior surstylus generally (at least in fresh material) dark brown, often more yellowish apically; in female, paired sclerites representing tergite 7 and sternite 7 shining black, each with short grey-pruinescent zone at posterior end; cercus of female brown, becoming black apically.

Head. Proportions resembling those of *Z. major* (D. McAlpine, 1982: figs 1–3); height of cheek c. 0.26–0.28 of height of eye; postvertical bristles slightly to strongly divergent. Antenna similar to that of *Z. minor* in proportions; arista c. 1.3–1.6 times as long as rest of antenna. Palpus only slightly thickened distally, where it is not more the c. 0.5 times as deep as cheek and at most very slightly deeper than prelabrum (i.e. very similar to palpus of *Z. minor*).

Thorax. Prosternum without precoxal bridge; chaetotaxy and most leg characters as for genus. Tibiae without any such enlarged dorsal or posterodorsal setulae or bristles as occur in *Z. clava* and *Z. johnsi*. Wing venation very similar to that of *Z. minor*, the little variation in contours and proportions apparently allowing no constant differences; cell-4 index = 0.55–0.61.

Abdomen. Sternite 1 deeply emarginate on posterior margin, almost divided in two; a pair of small sclerites

between sternite 1 and sternite 2 (these form part of segment 2 in *Z. minor* and *Z. major*); other preabdominal sternites broader than in *Z. minor*. Male: anterior surstylus much broader than that of *Z. minor*, neither broadened basally nor significantly tapered distally; posterior surstylus finely pointed at apex, with some long setulae, but these relatively sparse, without anterior gibbosity. Female: sternites 2 to 5 all broader than long; sternite 6 large, undivided; tergite 6 as long as tergite 5, with median desclerotization on posterior margin less extensive than in *Z. major*, and posterolateral angle not produced as in that species; paired sclerites of sternite 7 very narrow, separated by more than 4× width of each; paired sclerites of tergite 7 (Fig. 77) relatively large, each more than twice as long as wide, separated by well defined membranous median zone.

Dimensions (dried, some with abdomen artificially extended, parts behind tergite 6 excluded in ♀). Total length, ♂ 1.7–2.1 mm, ♀ 1.9–2.3 mm; length of thorax, ♂ 0.72–0.86 mm, ♀ 0.75–0.99 mm; length of wing, ♂ 1.8–2.0 mm, ♀ 2.0–2.4 mm; width of epandrium 0.26–0.29 mm.

Distribution. New South Wales: sea coast from Taree district to Sydney Harbour, between c. 32°00'S and 34°02'S. *Zalea dayi* may prove to have a wider distribution, especially as old dried specimens can be difficult to distinguish from *Z. minor*. However, recently made collections of *Zalea* from more northern localities in New South Wales and from eastern Tasmania include no *Z. dayi*.

Notes

Zalea dayi, though similar in size and superficial features to *Z. minor*, is sharply differentiated from all other Australian *Zalea* species in abdominal characters. In the male, the broad, almost parallel-sided dull brown anterior surstylus and apically pointed posterior surstylus are distinctive. In the female, the very narrow, widely separated paired sclerites of sternite 7, and the large, but elongate, largely shining black, well separated sclerites of tergite 7 are also distinctive; the much broader abdominal sternites 2 to 6 differentiate it from the sympatric *Z. minor* and *Z. major*.

The specific epithet refers to Barry J. Day, from whose material I first recognized the distinction of this species.

Genus *Suffomyia* Freidberg

Suffomyia Freidberg, 1995: 448. Type species (original designation) *S. scutellaris* Freidberg.

Diagnostic description. Minute flies; wing c. 0.9–1.5 mm long.

Head. Postvertical bristles proclinate, divergent; postfrons without setulae, except sometimes for a few between ocelli. Arista three-segmented, or two-segmented through loss of segment 4.

Thorax. Prothoracic precoxal bridge absent; posterior acrostichal setulae present or absent; prescutellar acrostichal bristle at most weakly differentiated; scutellum with or without two pairs of minor bristles in addition to two major pairs. Mid femur without posteroventral comb in either sex. Distal section of subcosta (beyond humeral crossvein) well sclerotized on c. middle third, weakened towards base, obsolete and unpigmented on c. distal third, thus ending freely in membrane well before subcostal break of costa; anterior crossvein meeting vein 4 distinctly basad of mid-length of discal cell; basal section of vein 4, separating first basal and second basal cells, quite desclerotized; alula narrowed distally, its terminal margin narrowly rounded, setulae of its marginal fringe c. as long as maximum width of alula.

Abdomen of male. Dorsal protandrial sclerite two to three times as long as tergite 5; only one pair of surstyli present, each with two condyles (one anterior, one posterior) where it hinges with margin of epandrium; distiphallus (only known for *S. scutellaris*) very short, apparently without associated papillae.

Abdomen of female (unknown in *S. ismayi*). Tergite 7 without anterior apodeme.

Distribution. Palaearctic Region: Sinai (Egypt and Israel). Australasian Region: Caroline Islands; New Guinea.

Notes

With the addition of two species to the only previously recognized representative, some of the previously used generic characters are seen to have only specific value, e.g., the shape of the head and antenna, the reduction of the acrostichal bristles and setulae, the number of scutellar bristles, some aspects of sclerotization of the female postabdomen, and the degree of proximal narrowing of the wing. As my research has shown additional differences between *Suffomyia* and *Zalea*, some probable differences awaiting confirmation from more material, and differences in range of character variation, I have set these out in the generic descriptions so that they may be readily contrasted.

I have experienced some difficulty in working with the old, dry, and, in one species, meagre material of these minute flies. My specific descriptions are therefore not as detailed as that of the type species given by Freidberg (1995), nor as those of most *Zalea* spp.

The following four apparent autapomorphies, not present in *Zalea*, support the monophyletic status of *Suffomyia*: postfrons without setulae between ocellar region and anterior margin; subcosta desclerotized distally; basal section of vein 4 desclerotized; in male, only one surstylus present, with two basal condyles.

Key to species of *Suffomyia*

1   Postgenal region without series of setulae near eye; scutellum with
two pairs of bristles only; male: epandrium setulose, but without
pair of outstanding bristles; surstylus bilobed .... *ismayi*

——— Postgenal region with a series of setulae near eye margin; scutellum
with two pairs of long bristles and two pairs of short bristles; male:
epandrium with one pair of long bristles; surstylus not bilobed 2

2   Costa with moderate-sized setulae between humeral and subcostal
breaks; antennal segment 3 subcircular, not longer than deep;
biseriate acrostichal setulae continued nearly to scutellar suture;
male: surstylus somewhat elongate and narrowed towards base;
female: tergite 7 large and undivided .... *sabroskyi*

——— Costa with one or two very long setulae between humeral and
subcostal breaks; antennal segment 3 c. 1.5 times as long as
deep; biseriate acrostichal setulae restricted to anterior half of
mesoscutum or almost so; male: surstylus subtriangular, widest
across base; female: tergite 7 divided into pair of widely separated
sclerites .... *scutellaris*
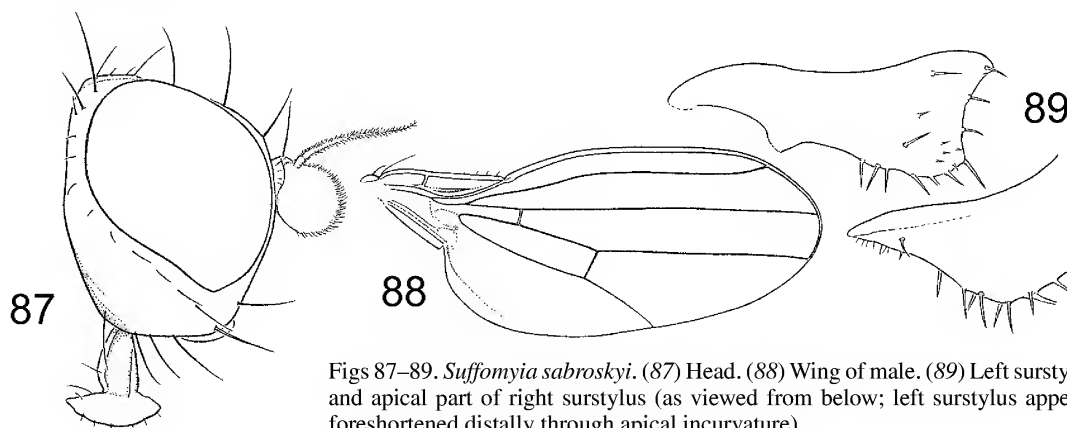
Figs 87–89. *Suffomyia sabroskyi*. (*87*) Head. (*88*) Wing of male. (*89*) Left surstylus and apical part of right surstylus (as viewed from below; left surstylus appears foreshortened distally through apical incurvature).

Suffomyia scutellaris Freidberg

Suffomyia scutellaris Freidberg, 1995: 448–454, figs 1–18.

Type material. HOLOTYPE ♂, Egypt: 10 km N of Nueiba, Sinai, 12.iv.1992, A.F. (TAU). Not seen by me.

Other material. See list of Freidberg (1995).

Notes

I saw material of this species in 1991 when I was sent specimens for comment, but I have not had further access to material for the present work. Freidberg's description gives excellent detail, and has enabled reasonable comparison with my two new *Suffomyia* spp.

Suffomyia sabroskyi n.sp.

Figs 19, 87–89

Material examined. HOLOTYPE ♂, Caroline Islands (Federated States of Micronesia): Giliman, Yap Island, 10.vi.1957, C.W.S. (BPB). Double-mounted on micro-pin. PARATYPES. Caroline Islands: 1♂, 5♀♀, same data as holotype (AM, BPB); 5♂♂, 3♀♀, Rumung Island, Yap Group, 19.vi.1957, at light, C.W.S. (AM, BPB).

Description (♂, ♀). General characters as given above for subfamily and for genus *Suffomyia*; somewhat resembling *S. scutellaris* as descried by Freidberg (1995).

Coloration (material slightly faded). Head brown, with covering of grey pruinescence, paler on face, anterior part of cheek, and parafacial; anterior margin of postfrons yellow; bristles black. Antenna dull tawny; segment 3 and arista largely brown. Palpus pale yellow, without dark setulae. Thorax grey, with brownish tinge; bristles black. Wing greyish hyaline, slightly darker in costal and marginal cells and part of submarginal cell (this pigmentation perhaps forming a brownish costal band in fresh material). Halter tawny. Abdomen greyish brown, with tergites almost uniformly coloured in male, often with irregular paler zones in female.

Head oval in profile, narrowed below; eye large, oblique, in profile occupying much more than half visible area of head; parafacial very narrow; postfrons c. 1.2–1.5 times as long as width at mid-length, and c. 0.37–0.43 times as wide as head; height of cheek c. 0.2 of height of eye; postgenal bristles forming a series near posteroventral margin of eye. Antenna: segment 3 smaller than in *S. scutellaris*, not distinctly longer than deep; arista two-segmented. Palpus smaller and less strongly clavate than in *S. scutellaris*.

Thorax. Scutellum shorter and more nearly semicircular than in *S. scutellaris*; thoracic chaetotaxy generally as for

other Zaleinae; four dorsocentral bristles often not all much larger than adjacent setulae; acrostichal setulae biserate, extending most of length of mesoscutum, often somewhat irregular, one or sometimes two hindmost pairs often (not always) largest so that pair of prescutellar bristles may be differentiated; mesopleuron with one relatively large mid-posterior bristle, dorsally directed posterodorsal setula, and several other slightly variable setulae; scutellum with two pairs of major bristles, pair of somewhat shorter mid-dorsal bristles and pair of still shorter, often crossed apical bristles. Fore femur with two to four posteroventral bristles and shorter or less distinct dorsal bristles; mid femur with several irregularly enlarged anterior setulae and few short, well spaced posteroventral bristles or setulae; hind femur coarsely setulose on anterior surface; all tibiae with some enlarged dorsal setulae, often as long as diameter of tibia; fore basitarsus with some setulae apparently apically bifid, almost straight (SEM not used). Wing not noticeably narrowed across anal region, but generally slightly narrower in female than in male; distal sections of veins 3 and 4 almost parallel; cell-4 index = 0.36–0.47.

Abdomen. Male: dorsal protandrial sclerite as long as tergites 3–5 combined, its anterior section (tergite 6) setulose, more than twice as long as bare posterior section (sternite 8); epandrium compact, rounded, with few setulae and two pairs of longer bristles, produced into small rounded lobe at anterolateral angle; surstylus somewhat elongate, subcrescentic, slightly narrowed towards the very oblique base, apically acute, with anterior margin much thickened on whole length, with setulae of various sizes including a few large, thickened ones on inner surface not shown in Fig. 89; aedeagal apodeme very long, extending into anterior part of abdomen; cercus shorter than in *S. ismayi.* Female: tergite 7 relatively large, undivided; sternite 7 present, apparently divided into two narrow sclerites.

Dimensions. Total length, ♂ 1.0–1.3 mm, ♀ 1.4–1.6 mm; length of thorax, ♂ 0.47–0.58 mm, ♀ 0.55–0.64 mm; length of wing, ♂ 1.1–1.3 mm, ♀ 1.3–1.5 mm.

Distribution. Micronesia: Yap Group, Caroline Islands.

Notes

Suffomyia sabroskyi can be distinguished from *S. scutellaris* by the shorter antennal segment 3, shorter non-spatulate palpus, shorter, more rounded scutellum, and by other characters given in the key.

The specific epithet refers to the late Curtis W. Sabrosky, who collected the type series.

Suffomyia ismayi n.sp.

Figs 90, 91

Material examined. HOLOTYPE ♂, Papua New Guinea: S of Idler Bay, Central Province, 14.xii.1980... "Swept decaying seaweed", J.W.I. (AM). Double-mounted on micro-pin. PARATYPES. 2♂ ♂, same data as holotype (AM, one to be later placed in a Papua New Guinea institution). One paratype has been cleared in lactic acid, and is now preserved in glycerol.

Description (♂, ♀ unknown). Somewhat resembling *S. sabroskyi* and agreeing with description of that species except as indicated below.

Coloration. Head largely grey-pruinescent; postfrons tawny, becoming grey posteriorly; face, parafacial, and cheek (except posterior part) pale yellowish. Antenna tawny; arista dark brown. Wing entirely pale, translucent, without pigmented areas of membrane; veins brownish yellow. Halter yellow.

Head, in profile (Fig. 90) less oval and ventrally narrowed than in *S. sabroskyi*; eye larger than in *S. scutellaris,* but smaller than in *S. sabroskyi*; postfrons broader than in that species; proportions of parts of head capsule approximately as in Fig. 90 (measurements not given because of distortion of all specimens); postgenal region without setulae. Antenna resembling that of *S. sabroskyi*; segment 4 much reduced but visibly sclerotized; segment 5 notably larger than in *S. sabroskyi.*

Thorax. Scutellum similar in shape to that of *S. sabroskyi,* with two bristle pairs only; acrostichal setulae well developed, but hindmost not enlarged, slightly in advance of hindmost dorsocentral; bristling of mesopleuron obscured by pin. Fore femur with one prominent posteroventral bristle near apical quarter, with dorsal setulae not much enlarged, but variable; fore tibia with dorsal setulae only slightly enlarged; mid femur with anterior setulae only slightly enlarged, with few distinct posteroventral bristles; mid and hind tibiae without enlarged setulae; hind femur with few slightly enlarged anterior setulae distally; fore basitarsus apparently without bifid setulae (confirmation with SEM desirable); claws very slender, falcate, not compressed (CLM). Wing slightly more narrowed across anal region than in *S. sabroskyi*; veins 3 and 4 very slightly diverging distally; cell-4 index = 0.34; ultimate section of vein 5 c. 1.2 times as long as penultimate section of vein 4.

Abdomen. Tergites 3, 4, and 5 of approximately similar length; dorsal protandrial sclerite 2.7 times as long as tergite 5; epandrium coarsely setulose, but without pair of outstanding bristles, with thickened ventral and anterior margins, thickening of anterior margin broadly interrupted medially; surstylus unequally bilobed, with larger, anterior lobe asymmetrically emarginate apically, posterior surface of surstylus in part densely pubescent, anterior margin with sparse fine setulae, but spinescent setulae (as in *S. scutellaris*)
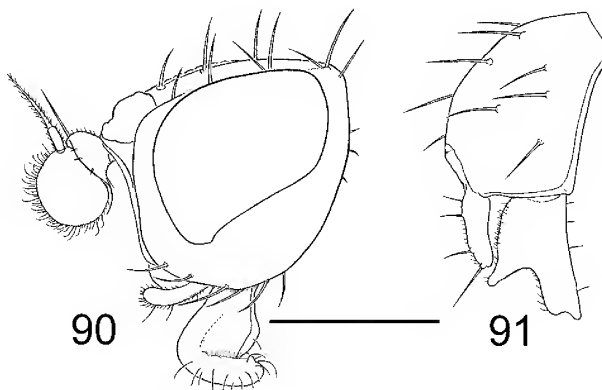
Figs 90, 91. *Suffomyia ismayi.* (*90*) Head (ptilinum partly exposed). (*91*) Epandriufm and associated parts from right side. Scale = 0.1 mm.

absent; basal articulation not oblique, with two condyles (anterior and posterior) as in *S. scutellaris*; cercus moderately long, with pubescence and few long setulae.

Dimensions. Total length 0.91–0.92 mm; length of thorax 0.40–0.47 mm; length of wing 0.88–0.96 mm.

Distribution. New Guinea: southeast coast.

Notes

Suffomyia ismayi is apparently the smallest fly in the Zaleinae, though precise dimensions were not given for *S. scutellaris*. In the absence of seriate postgenal setulae, it resembles most *Zalea* species, rather than the other *Suffomyia* species, but in *Z. earlyi* and *Z. wisei* the unusually long setulae of the (upper) postocular series are continued further ventrally than in other *Zalea* spp., and in *Z. johnsi* there is sometimes a rudimentary upper postgenal series.

In addition to the characters given in the key to species, *S. ismayi* differs from the other *Suffomyia* species and from other known zaleines in its simple, slender claws. As it shares apparent synapomorphies with other *Suffomyia* spp., and as the total number of known species is small, I consider it best to keep it in the same genus.

The specific epithet refers to John W. Ismay, who collected the type series.

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